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Martes: Taxonomy, Ecology, Techniques, and Management

EDITED BY

Gilbert Proulx
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Martes: Taxonomy, Ecology, Techniques, and Management

Fisher and American marten. Drawing by Gilbert Proulx.

Martes: Taxonomy, Ecology, Techniques, and Management

Proceedings of the Second International *Martes* Symposium

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This book is dedicated

to

Marjorie (Midge) Strickland

1931-1995

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PREFACE

Martes is an important genus of small carnivores belonging to the family Mustelidae. *Martes* includes the Eurasian (European) pine marten (*Martes martes*), the sable (*M. zibellina*), the Japanese marten (*M. melampus*), the American marten (*M. americana*), the stone (beech, house) marten (*M. foina*), the yellow-throated marten (*M. flavigula*), and the fisher (*M. pennanti*). These common names and scientific nomenclature are used throughout this book and follow Buskirk (1994).

The first symposium on the biology and conservation of martens, sables and fishers was held at the University of Wyoming in 1991. This was an opportunity for many scientists and students to meet, assess the state of our knowledge, and determine future research needs. The resulting publication (Buskirk et al. 1994) was a comprehensive review of the biology and conservation of martens, sables and fishers. The first symposium was also the catalyst for the creation of a *Martes* Working Group through which researchers and managers from several continents exchange information. After the first *Martes* symposium, scientists knew the limits of their knowledge and had identified areas where more research was required to better understand the biology of these carnivores and ensure their conservation.

The Second International *Martes* Symposium was held at the University of Alberta in August 1995. This symposium had over 100 participants and more than 70 papers and posters were presented. This second symposium was the precursor of this book, which is a proceedings rather than a review. Contributed papers were reviewed by at least two referees and accepted manuscripts received editorial guidance that emphasized clarity of expression and consistency of style and format.

Although this book considers the entire genus, most of its 31 papers deal with the American marten and/or the fisher. Papers are separated into five categories. Those in Part I pertain to the intra- and interspecific morphometrics and phylogenetic relationships of *Martes*. Part II focuses on the reproductive and survival rates of the American marten and the fisher, and the behavior of the American and stone martens during the reproductive season. Papers on habitat characteristics and utilization are presented in Part III. The spatial and temporal use of habitats at the stand and landscape levels is discussed according to such factors as denning and resting sites, prey populations and snow depths. Scientists continue to refine their research and management techniques and to identify better ways to effectively capture and study martens, fishers and sables. Some of these new techniques are presented in Part IV. Finally, with a better understanding of populations and habitats, several researchers have attempted to integrate *Martes* into forest management. Socio-economic aspects, modelling and the assessment of

the impact of timber harvesting on American marten populations are discussed in Part V.

The originality and diversity of the papers presented here show how important the genus *Martes* is to naturalists, zoologists, wildlife managers, and foresters. There is still much to be learned about this genus and we hope this book will be another important tool used by the scientific community and the interested public in the further study and conservation of martens, fishers and sables.

Gilbert Proulx
Harold N. Bryant
Paul M. Woodard

Literature Cited

Buskirk, S. W. 1994. Introduction to the genus *Martes*. Pages 1-10 in S. W. Buskirk, A. S. Harestad, M. G. Raphael, and R. A. Powell, eds. Martens, sables, and fishers. Biology and conservation. Cornell University Press, Ithaca, New York.

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Part I

Taxonomy, Genetics, and Morphology

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PHYLOGENETIC RELATIONSHIPS WITHIN *MARTES* BASED ON NUCLEAR RIBOSOMAL DNA AND MITOCHONDRIAL DNA

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Abstract: Restriction fragment length polymorphism (RFLP) in the spacer regions of the nuclear ribosomal DNA (rDNA) and sequence variations in mitochondrial DNA were examined in 4 species in the genus *Martes*: the Japanese marten (*M. melampus*), the sable (*M. zibellina*) from Japan and from Russia, the American marten (*M. americana*) from North America, and the yellow-throated marten (*M. flavigula*) from China. The RFLPs of rDNA showed that interspecies diversity among *M. melampus*, *M. zibellina*, and *M. americana* was small with 0.1%-0.4% estimated sequence divergence. This divergence indicates that speciation occurred during the late Pleistocene. Sequence divergence between these three species and *M. flavigula* based on rDNA-RFLP was 2.5%-2.9%, suggesting that divergence occurred during the early Pliocene. We sequenced the 402-bp portion of the mitochondrial cytochrome *b* gene for the 4 species of martens. Sequence divergences between *M. melampus* and *M. zibellina*, *M. americana*, and *M. flavigula* were 2.8%, 3.6%, and 14.4%, respectively. Assuming that the divergence

rate of the cytochrome *b* gene is 2.5% per million years per pair of lineages, divergence of the mtDNA of *M. flavigula* and those of the other three species was approximately 6 million years ago, which corroborates the data from rDNA-RFLP. However, the amount of divergence among the mtDNAs of these three species was slightly greater than that of rDNA-RFLPs. These data suggest that genetic exchange continued intermittently during the Pleistocene after the geographic isolation of Japan nearly 2 million years ago.

Introduction

The Japanese islands have been intermittently attached directly to the Eurasian Continent, and indirectly to the North American Continent, by land bridges during the Pleistocene ice ages of the past 2 million years. Many migrations of mammalian species from these continents to Japan have occurred. For this reason the evolutionary history of these mammalian species is thought to be complex.

Two species in the genus *Martes* occur in Japan: the sable (*M. zibellina*) in Hokkaido, and the Japanese marten (*M. melampus*) in Honshu, Shikoku, Kyushu, and Tsushima Islands. However, the origin of the 2 species has not yet been conclusively determined. Previous evolutionary studies have been based primarily on morphological characteristics. In *M. zibellina*, morphological analysis indicates that there is little difference between populations in Hokkaido and the northern part of the Asian Continent. Thus, it has been suggested that the population in Hokkaido became isolated from the continental population quite recently, probably in the Late Pleistocene.

Morphologically, *M. melampus* and *M. zibellina* are similar to *M. americana,* which occurs in North America (Anderson 1970). By contrast, another Asian species, *M. flavigula*, which occurs from India through China to Korea, is considered to be morphologically divergent from the aforementioned species (Anderson 1970, Buskirk 1994).

To trace the evolutionary history of these species and to estimate their time of divergence, analysis of fossil specimens would be useful. However, fossils are generally rare because martens have always been forest dwellers and small (Buskirk 1994). Available fossil data on the Japanese martens are so scarce that a comprehensive phylogenetic study is not possible.

Recently, other approaches including chromosomal (Obara 1991) and molecular analyses (Wayne et al. 1991; Masuda and Yoshida 1994a, b) have been used, but these studies were not conducted to compare the variation between continental and Japanese populations or species.

In the past 2 decades, quantitative phylogenetic analyses of related species of mammals have been performed based on variations in cytoplasmic and nuclear genomes. Mitochondrial DNA (mtDNA) is located in the cytoplasm and is maternally inherited. Thus, if we analyze the mtDNA patterns of natural populations,

we can obtain information about the migration and dispersion of females, but not males. The data from mtDNA should be supplemented with that from nuclear genes. Restriction enzyme fragment length polymorphism (RFLP) of the spacer regions of ribosomal DNA (rDNA) is also a good tool for estimating phylogenetic relationships among related species (Arnheim et al. 1980; Suzuki et al. 1986, 1987, 1990, 1994a, b; Hosoda et al. 1993; Lan et al. 1993).

The rDNA locus is a multigene family that consists of several hundred copies. Each unit is composed of the coding regions (around 10 kb) for evolutionally highly conservative rRNA (18S, 5.8S, 28S) and the spacer regions (around 30 kb) that connect the coding regions. The former are most useful as probe regions; the latter evolve rapidly and, in many cases, have polymorphic restriction sites. Thus the spacer regions might be used to learn about genetic relationships among related species.

In this study we analyzed variation in both mtDNA and rDNA in 4 species of martens, *M. melampus*, *M. zibellina*, *M. americana*, and *M. flavigula*. We consider the origin of the Japanese marten, *M. melampus*, and the sable, *M. zibellina*, in Hokkaido.

Materials and Methods

Extraction of DNA

The species and geographic origins of the animals used in this study are listed in Table 1. DNA was extracted from the liver as described by Maniatis et al. (1982).

Analysis of rDNA RFLP

In order to construct restriction maps of the various types of rDNA repeating units, the genomic DNA of 6 species (7 individuals) of mustelids was digested with 12 restriction enzymes: *Aat*I, *Bam*HI, *Bcl*I, *Bgl*II, *Dra*I, *Eco*RI, *Hin*dIII, *Kpn*I, *Pst*I, *Pvu*II, *Sac*I and *Xba*I. The digested DNA on nylon filters were hybridized sequentially with 3 (^{32}P)-labeled rDNA probes. The 3 probes were designated 28S (0.7 kb of DNA, including the 3' end of the gene for 28S rRNA), 18S (0.9 kb of DNA, including the 5' end of the gene for 18S rRNA), and INT (6.6 kb of DNA, consisting of the *Eco*RI fragment from E1 to E2). These probes were prepared from clones of mouse rDNA as described by Kominami et al. (1981, 1982).

Direct Sequencing Analysis of mtDNA

Semi-nested PCR and direct sequencing were performed according to the manufacturer's instructions (ABI, Division of Applied Biosystems, Perkin Elmer). The entire 1.1-kb sequence of the cytochrome *b* gene was amplified by the first PCR using the L14724 and H15915 primers of Kocher et al. (1989). The

Table 1. Specimens analyzed in this study.

Species	Code	Common name	Collection locality
Martes zibellina	Mzi1	sable	Khabarovsk, Russia
Martes zibellina	Mzi2	sable	Hokkaido, Japan
Martes melampus	Mme	Japanese marten	Wakayama, Japan
Martes americana	Mam	American marten	Maine, USA
Martes flavigula	Mfl	yellow-throated marten	Yunnan, China
Mustela nivalis	Mni	least weasel	Hokkaido, Japan
Mustela sibirica	Msi	Siberian weasel	Yunnan, China

amplified fragments were sequenced with the automated sequencer using appropriate sequence primers.

Sequencing of the mitochondrial gene for 12S rRNA and its 5' flanking region was carried out in the same way as the cytochrome *b* gene analysis. A 0.9-kb fragment of the 12S rRNA gene and the 5' flanking region were amplified by PCR using the L613 and H1478 primers (Kocher et al. 1989).

Construction of Phylogenetic Trees

We compared the arrangement of restriction sites between pairs of rDNA types and counted the common and different sites and fragments. Employing the method developed by Gotoh et al. (1979), in which backward and parallel mutations are taken into account (Jukes and Cantor 1969), we produced a matrix of sequence divergences for all possible combinations of repeating unit types (Table 2). We produced a matrix of sequence divergence for all possible combinations of mtDNA sequences (Table 3) using the computer program DNADIST in PHYLIP 3.5 (Felsenstein 1993). We constructed phylogenetic trees using the neighbor-joining (NJ) method (Saitou and Nei 1987) using the computer program NEIGHBOR

Table 2. Sequence divergences (%, upper right) among the major repeating unit types of rDNA from 6 species of Mustelidae, based on numbers of common and different restriction sites (lower left). Abbreviations as in Table 1.

Species	Mzi	Mme	Mam	Mfl	Mni	Msi
Mzi	-	0.3	0.4	2.9	5.7	7.2
Mme	28/1	-	0.1	2.5	5.7	6.5
Mam	27.5/1.5	28.5/0.5	-	2.7	5.4	6.1
Mfl	21/8	22/7	21.5/7.5	-	6.8	5.4
Mni	16/13	16/13	16.5/12.5	14/14	-	2.1
Msi	14/15	15/14	15.5/13.5	16/12	22/6	-

Table 3. Sequence divergences (%) of the mtDNA cytochrome *b* gene (402 bp) in 6 mustelid species. Abbreviations as in Table 1.

Species	Mzi2	Mme	Mam	Mfl	Mni	Msi
Mzi1	1.3	2.8	4.9	14.7	13.6	15.7
Mzi2		3.6	6.2	14.7	13.3	16.0
Mme			3.6	14.4	11.9	14.2
Mam				15.0	13.6	14.8
Mfl					16.9	20.0
Mni						10.1

in PHYLIP 3.5. Based on the presence or absence of each restriction site, we produced a phylogenetic tree by maximum parsimony using the MIX program, with the "Wagner" option in PHYLIP. Confidence levels for each grouping were calculated using the bootstrap program SEQBOOT, with 500 replications, in PHYLIP. The tree was produced using the CONSENCE program in PHYLIP.

Results

Variation of rDNA

The 17 restriction sites in the coding regions, as well as the *Dra*I and *Kpn*I sites in the internal spacers, showed no intra- and interspecies differentiation, as observed in other mammalian species (Suzuki et al. 1990, Hosoda et al. 1993). By contrast, some of the restriction sites in the external spacer regions were polymorphic within and between species.

Only one restriction site, *Bgl*II located upstream from the 5' end of the 18S gene, was polymorphic between the Japanese marten (Mme) and the sable (Mzi). We did not see any intraspecific divergence between the Russian sable and the Hokkaido sable in the types of rDNA. Similarly, only 1 restriction site, a *Sac*I located upstream from the 5' end of the 18S gene, differed between the American marten and the Japanese marten. By contrast, the repeating type of the yellow-throated marten (Mfl) differed from those of the sable (Mzi), the Japanese marten (Mme), and the American marten (Mam), at 7 to 8 restriction sites in the spacer regions. The extent of divergence was similar to that between the 2 species of *Mustela*, the Siberian weasel (*M. sibirica*, Msi) and the least weasel (*M. nivalis*, Mni) (Table 2).

Construction of Phylogenetic Trees from rDNA

Using the sequence divergences we constructed a phylogenetic tree by the NJ method (Fig. 1a). In addition, by considering the presence or absence of each of 49 restriction sites that were polymorphic among the 6 species examined, we

constructed a phylogenetic tree by the maximum parsimony method (Fig. 1b). The topology was identical to that of the NJ tree.

Variation of mtDNA and Construction of a Phylogenetic Tree

We also used the PCR direct sequence method to determine the nucleotide sequence of 402 bp of the mitochondrial cytochrome *b* gene in the 6 species (7 individuals) listed in Table 1. We produced a matrix of sequence divergence (Table 3) for all possible combinations of mtDNA sequences (Fig. 2) using DNADIST in PHYLIP 3.5. The phylogenetic tree of cytochrome *b* nucleotide sequences was constructed by the NJ method (Fig. 3). The sequence divergences among the 4 species of *Martes* were large (around 15%), making it difficult to

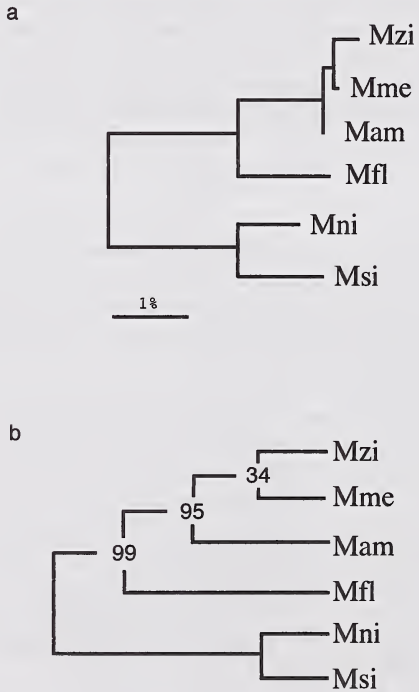

Figure 1. Phylogenetic trees based on the major rDNA repeating unit types from the 6 species as determined by the neighbor-joining (a), and maximum parsimony (b) methods. The bootstrap percentages are given for the maximum parsimony tree. Abbreviations as in Table 1.

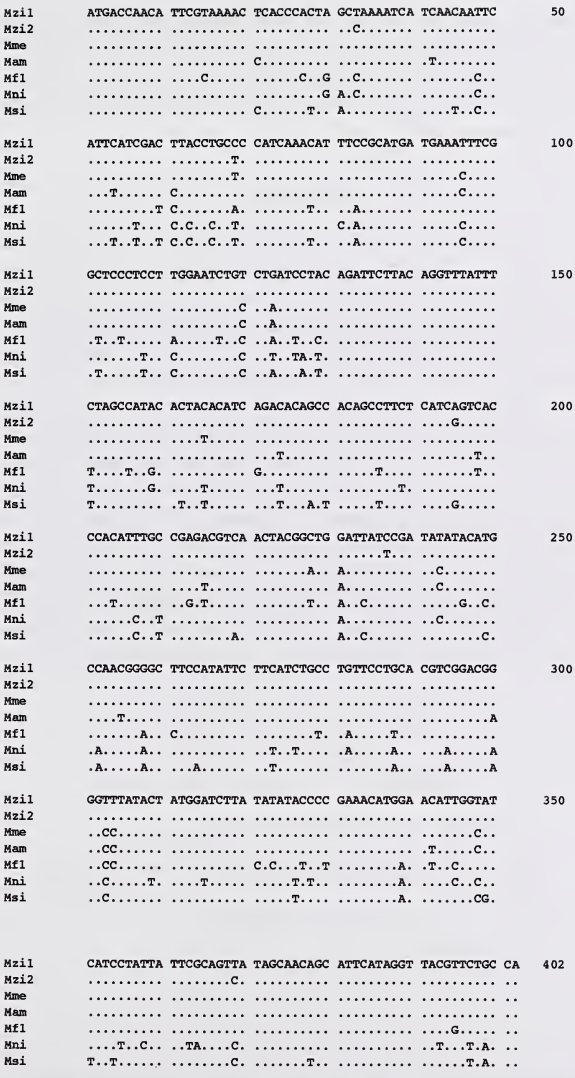
Mzi1 ATGACCAACA TTCGTAAAAC TCACCCACTA GCTAAAATCA TCAACAATTC 50
Mzi2 ....C..... .....
Mme ....
Mam .... C..... ..... .T.....
Mfl ....C..... .....C..G ..C..... .....C..
Mni ....G A.C..... .....C..
Msi .... C.....T.. A..... ....T..C..
Mzi1 ATTCATCGAC TTACCTGCCC CATCAAACAT TTCCGCATGA TGAAATTTCG 100
Mzi2 ....T. ....
Mme ....T. ....C....
Mam ...T..... C..... ....C....
Mfl .....T C.....A. .....T.. ..A..... .....
Mni .....T... C.C..C..T. ..... C.A..... .....C....
Msi ...T..T..T C.C..C..T. .....T.. ..A..... .....C....
Mzi1 GCTCCCTCCT TGGAATCTGT CTGATCCTAC AGATTCTTAC AGGTTTATTT 150
Mzi2 ....
Mme ....C ..A..... ....
Mam ....C ..A..... ....
Mfl .T..T..... A.....T..C ..A..T..C. ....
Mni .....T.. C.....C ..T..TA.T. ....
Msi .T.....T.. C.....C ..A...A.T. ....
Mzi1 CTAGCCATAC ACTACACATC AGACACAGCC ACAGCCTTCT CATCAGTCAC 200
Mzi2 ....G.....
Mme ....T..... ....
Mam ....T..... ....T..
Mfl T....T..G. ..... G..... .....T..... .....T..
Mni T.....G. ....T..... ...T..... .....T. .....
Msi T..... .T..T..... ...T...A.T .....T.... ....G.....
Mzi1 CCACATTTGC CGAGACGTCA ACTACGGCTG GATTATCCGA TATATACATG 250
Mzi2 ....T... .....
Mme ....A.. A..... ..C.....
Mam ....T..... ..... A..... ..C.....
Mfl ...T..... ..G.T..... .....T.. A..C..... .....G..C.
Mni .....C..T .... A..... ..C.....
Msi .....C..T .....A. ..... A..C..... .....C.
Mzi1 CCAACGGGGC TTCCATATTC TTCATCTGCC TGTTCCTGCA CGTCGGACGG 300
Mzi2 ....
Mme ....
Mam ....T..... ....A
Mfl .....A.. C..... .....T. .A.....T.. .....
Mni .A.....A.. ....T..T.... .A.....A.. ...A.....A
Msi .A.....A.. ...A..... ..T..... .....A.. ...A.....A
Mzi1 GGTTTATACT ATGGATCTTA TATATACCCC GAAACATGGA ACATTGGTAT 350
Mzi2 ....
Mme ..CC..... ....C..
Mam ..CC..... .... .T.....C..
Mfl ..CC..... ..... C.C...T..T .....A. .T..C.....
Mni ..C.....T. ....T..... .....T.T.. .....A. ....C..C..
Msi ..C..... ....T.... .....A. .....CG.
Mzi1 CATCCTATTA TTCGCAGTTA TAGCAACAGC ATTCATAGGT TACGTTCTGC CA 402
Mzi2 ....C. ....
Mme ....
Mam ....
Mfl ....G..... ..
Mni ....T..C.. ..TA....C. ....T...T.A. ..
Msi T..T..... .....C. .....T.. ....T.A. ..

Figure 2. Alignment of the 5' portion of the gene for cytochrome *b* from 7 individuals of 4 *Martes* and 2 *Mustela* species. Abbreviations as in Table 1.

trace phylogeny using this rapidly evolving mtDNA cytochrome *b* gene. We attempted to analyze a partial sequence (452 bp) of the mitochondrial 12S rRNA gene in 5 of the species (Table 4). A phylogenetic tree constructed by the NJ method is shown in Figure 4. The topology is identical to that of the tree based on the cytochrome *b* gene.

Discussion

In this study, we used 3 types of molecular markers, the cytochrome *b* gene, 12S rRNA, and nuclear rDNA, to examine the phylogenetic relationships among 4 species in *Martes*. We found that *M. melampus*, *M. zibellina*, and *M. americana* were closely related to each other and that these 3 species were much more distant from *M. flavigula*. The estimated time of divergence between *M. flavigula* and the other 3 species of *Martes* was nearly the same in the analyses of both mtDNA and rDNA. The sequence divergence of the mitochondrial cytochrome *b* gene was 14-15% (Table 3) and the time of divergence is estimated at 5-6 million years ago (mya) if we assume that the cytochrome *b* gene diverges at a rate of 2.5% per million years (myr) per pair of lineages in mammals (Meyer et al. 1990, Irwin et al. 1991, Masuda et al. 1994a). The sequence divergence in the mitochondrial 12S rDNA between *M. flavigula* and *M. zibellina* is 6% (Table 4). The evolutionary rate of the 12S gene is uncertain but the extent of the divergence is comparable to that between *Felis catus* (Lopez et al, unpublished data) and *F. concolor* (Springer et al. 1995), in which divergence time is thought to be 10

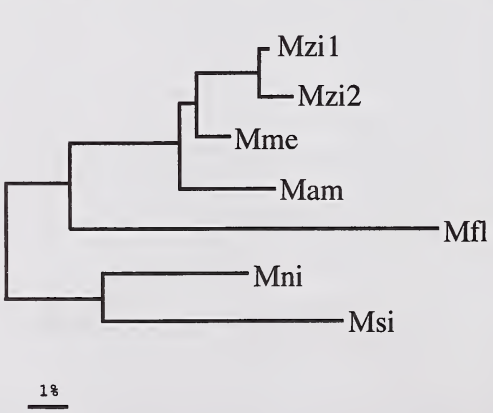

Figure 3. Phylogenetic tree based on the cytochrome b sequences from 7 individuals of 4 *Martes* and 2 *Mustela* species. Abbreviations as in Table 1.

Table 4. Sequence divergences (%) of the mitochondrial 12S rDNA gene and its 5' flanking sequence (453 bp) in 5 mustelid species. Abbreviations as in Table 1.

Species	Mme	Mfl	Mni	Msi
Mzi	0.9	5.5	10.3	9.1
Mme		6.0	11.0	9.8
Mfl			10.8	10.4
Mni				6.4

mya (Macdonald 1992). The sequence divergence of the rDNA spacer was 3-4% (Table 2) and the divergence time was estimated to be 3-4 mya if the rDNA spacer diverges at about 1% per myr per pair of lineages (Hosoda et al. 1993, Suzuki et al. 1994a, b). Thus we infer that *M. flavigula* diverged from the other 3 species early in the Pliocene. These results may cause reevaluation of the previous assumption that divergence between *M. flavigula* and the other species of marten, such as *M. melampus* or *M. zibellina*, occurred in the Miocene (20 mya), a conclusion based on fossil data (Anderson 1970).

Our data suggest that *M. zibellina*, *M. melampus*, and *M. americana* diverged simultaneously during the Pleistocene. These data confirm the previous conclusions of Hagmeier (1961) and Anderson (1970) who suggested on the basis of morphological and fossil data that there are many similarities among *M. martes*, *M. zibellina*, *M. melampus*, and *M. americana*. Fossils of *M. zibellina* have been discovered in the late Pleistocene of Eurasia (Anderson 1994). A small number of fossils of *M. melampus* have also been found in deposits of the same age in

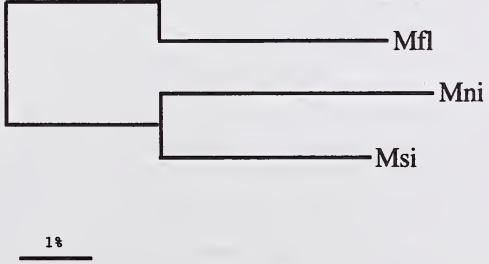

Figure 4. Phylogenetic tree based on the 12S rRNA from 5 individuals of 3 *Martes* and 2 *Mustela* species. Abbreviations as in Table 1.

Japan (Hasegawa et al. 1968). Anderson (1970, 1994) postulated that *Martes* reached Japan during the Pleistocene via the Kuril Islands from Kamtchatka and also from Sakhalin Island across the Soya Strait.

In contrast, there is considerable difference between the analyses of mtDNA and rDNA regarding the estimated time of divergence among *M. zibellina*, *M. melampus*, and *M. americana*. The range of the sequence divergences among these species was 2.8-6.2% for the cytochrome *b* gene (Table 3) and the divergence times were estimated at 1-2.5 mya assuming that the divergence rate is 2.5% per myr per pair of lineages. By contrast, the range of sequence divergences in the rDNA spacer was 0.1-0.4% (Table 2). If we assume that rDNA diverges at a rate of about 1% per myr, this result suggests that these 3 species diverged during the late Pleistocene. There are 2 ways to explain this discrepancy. First, the evolutionary relationships among the 3 species may have been somewhat complicated. Between the original colonization by the ancestral populations of northern Asia, including Japan, and North America, which occurred 2 mya, and the final isolation of these regions, perhaps 5000 years ago, there may have been continued genetic exchange, resulting in the homogenization of genes such as the nuclear rDNA and preservation of others such as the mtDNA. Second, the estimated divergence time based on these molecular markers may be overestimated, or underestimated in the cases of the *Martes* species considered here. The evolutionary rate of rDNA may be slower in these species for some unknown reason. Alternatively, the divergence of mtDNA may be overestimated compared to the divergence of the species. There are many cases where related species or populations preserve distinct mtDNA, which diverged at an older age prior to the divergence of species or populations.

Even if morphological analysis supports the former possibility (Anderson 1970), we should address this issue by examining additional genes in these species in future studies. It is very important that many molecular markers be examined in order to obtain reliable results.

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ARE THERE TWO SPECIES OF MARTEN IN NORTH AMERICA? GENETIC AND EVOLUTIONARY RELATIONSHIPS WITHIN *MARTES*

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Abstract: The American marten is currently considered a single species (*Martes americana*) that comprises a number of morphologically differentiated subspecies across North America. Two distinct subgroups are recognized: the *"americana"* group from eastern North America and the *"caurina"* group from the Pacific Northwest and the Great Plains. These groups were formerly recognized as distinct species, but because morphological intermediates were identified in areas of sympatry, the 2 forms have been considered a single species. Examination of mitochondrial cytochrome *b* DNA sequences identifies 2 genetically distinct clades whose geographic distributions correspond to the subspecies groups. Phylogenetic analysis of the 2 American groups, European marten (*M. martes*), sable (*M. zibellina*), Japanese marten (*M. melampus*), and fisher (*M. pennanti*) indicates that all are evolutionarily distinct lineages. The pairwise sequence divergence between the nearctic clades is about the same as those between palearctic species. The genetic analysis supports the hypothesis that the 2 North American subspecies groups should once again be considered 2 distinct species: *Martes americana* and *Martes caurina,* respectively. In combination with data on the yellow-throated marten (*M. flavigula*), these data strongly imply that *Martes* is of relatively young (early Pliocene) origin. Genetic data also support the monophyly of its 3 component subgenera, *Pekania* (= *M. pennanti*), *Charronia* (= *M. flavigula*), and *Martes* (all other extant species), with the first being the sister group to the latter 2. Endemic nearctic fishers and martens represent separate invasions of the New World.

Introduction

The American marten is a morphologically diverse mustelid carnivore whose taxonomy has been widely studied and debated (Hagmeier 1955, 1958; Hall 1981; Anderson 1994). Eastern forms, the first described, have been referred to *Martes americana* (Turton, 1806). Merriam (1890) subsequently described a larger form

of marten from the Cordillera of North America as a separate species, which he named *Mustela* (= *Martes*) *caurina*. However, Wright (1953) found evidence of morphological intergradation between these forms in several locations on the northern Great Plains and relegated the latter to subspecific rank; this practice has been followed ever since. Subsequent authors have continued to recognize that there are 2 morphologically distinct subspecies groups, a "*caurina*" group from the Pacific Coast and the Great Plains, and an "*americana*" group from the remaining eastern and northern part of the marten's range (Hagmeier 1955; Anderson 1970, 1994; Banfield 1974; Clark et al. 1987; Graham and Graham 1994).

American martens constitute the easternmost populations of the holarctic subgenus *Martes*, which extends from western Europe across Siberia into North America and includes *M. martes* (European pine marten), *M. foina* (beech or stone marten), *M. zibellina* (sable), and *M. melampus* (Japanese marten) (Anderson 1994). With the exception of *M. foina*, these species constitute a more or less continuous cline of steadily reduced size, and it has sometimes been suggested that they are conspecific (Hagmeier 1961, Anderson 1970).

We have been examining the genetics of the North American marten with a view toward improved management of the species, particularly the preservation of genetic biodiversity in reintroduced populations in Terra Nova National Park, Newfoundland (Hicks and Carr 1992, 1995). Here, we consider the implications of our data for the systematics of *Martes* in North America and elsewhere.

Materials and Methods

Tissue samples were obtained, and DNA was extracted, amplified *in vitro* by the polymerase chain reaction, and sequenced as previously described (Carr and Marshall 1991a,b; Hicks and Carr 1992, 1995). We used as amplification and sequencing primers a pair of primers that include a 401-base pair portion of the mitochondrial cytochrome *b* gene. Our data now include representatives of 12 of 14 subspecies of American marten as described by Hall (1981) (all except *sierrae* and *humboldtensis*) (Table 1, Fig. 1) as well as European pine marten (*M. martes*), sable (*M. zibellina*), and fisher (*M. pennanti*). The sequence from a homologous 375-base pair portion of the same gene from Japanese marten (*M. melampus*) was obtained from Masuda and Yoshida (1994). *M. pennanti* is the only member of the subgenus *Pekania*, and was therefore selected as the outgroup; all other species examined are placed in the subgenus *Martes*. Phylogenetic analyses were performed using PAUP version 3.1.1 (Swofford 1993). Maximum parsimony trees were identified with all substitutions weighted equally, the branch-and-bound search algorithm, and delayed character transformation optimization. Confidence limits on branches were estimated by bootstrap analysis with 1000 replicates, the heuristic search algorithm, 5 random taxon additions, and nearest-neighbor-interchange branch-swapping.

Table 1. Species and subspecies designation, geographic origin, sample size, and genotype of 18 specimens of *Martes americana* and *M. caurina* (cf. Hicks and Carr 1995).

Species and subspecies	Geographic origin	*n*	Genotype[a]
Martes americana:			
atrata	E Newfoundland	1	TNP
brumalis	E Labrador	1	TNP
americana	N New Brunswick	1	TNP
abieticola	N Manitoba	1	TNP
actuosa	Northwest Territories	2	TNP
kenaiensis	Kenai Peninsula, AK	2	TNP
abietinoides	Selkirk Range, BC	1	SEL
Martes caurina:			
caurina	SW British Columbia	2	VCI
vancouverensis	Vancouver Island, BC	2	VCI
nesophila	Queen Charlotte Island, BC	3	QCI
origenes	SE Wyoming	1	WYO
vulpina	N Idaho	1	WYO

[a] Each genotype has a unique base-pair sequence; see text.

Results

Nucleotide substitutions in the 401-base pair region define 6 genotypes in the North American martens examined, as well as unique genotypes in each of the other species. These genotypes have been submitted to the Genome Sequence Data Base and assigned the accession numbers L77952-L77961. The North American genotypes fall into 2 distinct groups. Martens representative of 6 subspecies from the eastern (*atrata*, *brumalis*, *americana*) and northern (*abieticola*, *actuosa*, and *kenaiensis*) portions of the range have identical genotypes (designated genotype TNP). A single marten from the Selkirk Mountains in southeastern British Columbia (subspecies *abietinoides*) has a genotype that differs from TNP by a single nucleotide substitution (genotype SEL). These 7 subspecies correspond to the eastern "*americana*" group recognized on morphological grounds (Anderson 1994). Martens representative of the 2 southern subspecies (*origenes* and *vulpina*) have identical genotypes that differ from the TNP genotype by 6 nucleotide substitutions (genotype WYO). Marten from the extreme western part

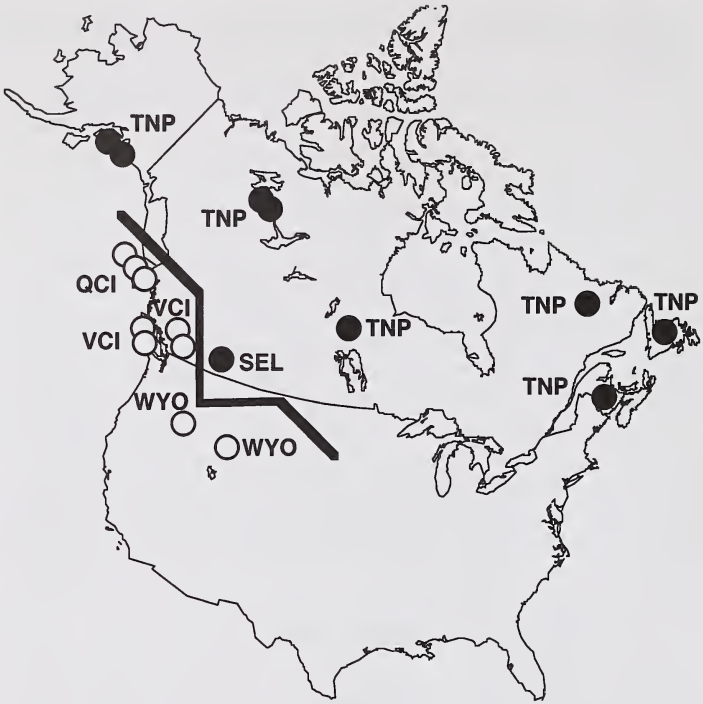

Figure 1. Geographic distribution of sample sites and genotypes in Table 1 (after Hicks and Carr 1995). The line indicates the approximate separation between *Martes americana* (closed circles) and *M. caurina* (open circles). The number of circles at each site indicates the sample size.

of the species' range in coastal British Columbia (*caurina*, *vancouverensis*, and *nesophila*) have genotypes that differ from the WYO genotype by single substitutions (genotype VCI in the first 2 subspecies, genotype QCI in the last). Along with subspecies *sierrae* and *humboldtensis*, these subspecies correspond to the western "*caurina*" group (Anderson 1994). In all subspecies represented by more than 1 individual, all DNA sequences were identical. Preliminary analysis of 2 individuals from the Sierra Nevada of California (subspecies *sierrae*) indicates that they share a distinct genotype that is more similar to genotypes in the western WYO/VCI/QCI group.

Parsimony analysis identifies a single minimum-length tree that requires 73 steps (consistency index 0.892). This tree separates the palearctic and nearctic genotypes, identifies *M. melampus* as the sister species to *M. martes* and *M. zibellina* among the palearctic species, and identifies 2 distinct clades, comprising genotypes TNP/SEL and genotypes WYO/VCI/QCI, respectively, within North American marten (Fig. 2). Bootstrap analysis supports all interspecific branches and those between TNP/SEL and WYO/VCI/QCI at greater than 80% confidence. Pairwise patristic differences (number of substitutions inferred from the reconstructed phylogenetic tree) between genotypes in the 2 nearctic clades range from 7 to 9 substitutions, as compared with 6 to 9 substitutions among palearctic species (Table 2). *M. pennanti* (subgenus *Pekania*) differs from members of the subgenus *Martes* by from 48 to 54 substitutions.

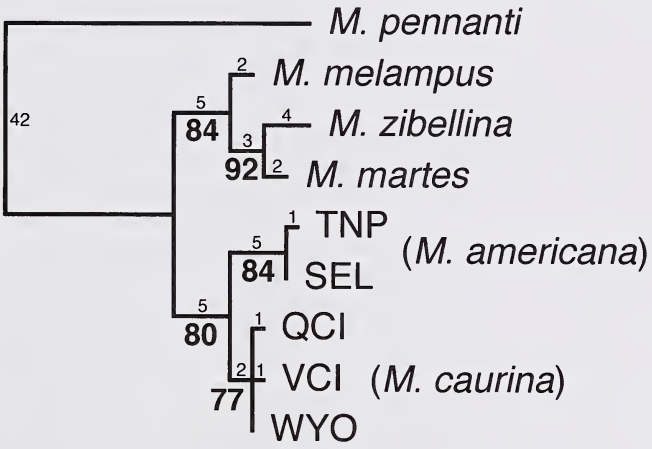

Figure 2. Phylogenetic tree (maximum parsimony) of mutational differences among mitochondrial cytochrome *b* genotypes in *Martes americana* (TNP and SEL), *M. caurina* (WYO, QCI, and VCI), *M. martes*, *M. zibellina*, and *M. melampus*. The tree is rooted with respect to the genotype of *M. pennanti*. Numbers above each branch indicate the inferred number of nucleotide substitutions that occur on that branch. Numbers in bold below each branch indicate the percent occurrence of that group in 1000 bootstrap replicates.

Table 2. Uncorrected proportional sequence differences (lower half matrix) and number of nucleotide substitutions (upper half matrix) among 9 genotypes from *Martes* spp. Genotypes TNP and SEL are assigned to *M. americana*; genotypes QCI, VCI, and WYO are assigned to *M. caurina* (see text). Data for *M. melampus* are taken from Masuda and Yoshida (1994).

	M. pennanti	***M. melampus***	***M. zibellina***	***M. martes***	**TNP**	**SEL**	**VCI**	**QCI**	**WYO**
M. pennanti		48	52	50	52	51	50	48	49
M. melampus	0.1203	-	9	7	12	11	13	13	12
M. zibellina	0.1303	0.0226	-	6	19	18	20	20	19
M. martes	0.1253	0.0175	0.0150	-	17	16	18	18	17
TNP	0.1303	0.0301	0.0476	0.0426	-	1	7	7	6
SEL	0.1278	0.0276	0.0451	0.0401	0.0025	-	8	8	7
VCI	0.1253	0.0326	0.0501	0.0451	0.0175	0.0200	-	2	1
QCI	0.1203	0.0326	0.0501	0.0451	0.0175	0.0200	0.0050	-	1
WYO	0.1228	0.0301	0.0476	0.0426	0.0150	0.0175	0.0025	0.0025	-

Discussion

Phylogenetic analysis of mitochondrial DNA sequences identifies two distinct genetic clades among North American marten. The distribution of these clades corresponds to the ranges of 2 groups that have been recognized on morphological grounds, namely the eastern and northern "*americana*" group and the southern and western "*caurina*" group. Pairwise sequence divergences between these groups are as great as those between Palearctic species of *Martes*. We suggest that the genetic data support the hypothesis that the "*americana*" and "*caurina*" groups of American marten are distinct species, *Martes americana* (Turton, 1806) and *Martes caurina* (Merriam, 1890).

The occurrence of 2 distinct species of marten in North America was generally recognized prior to the work of Wright (1953). Wright examined a contact zone between what would then have been called *M. americana abietinoides* and *M. caurina vulpina* in the region of the Swan, South Fork, and Sun rivers in western Montana. He reported evidence of individuals with intermediate morphology (based on the greatest length of the skull and the size of the auditory bullae). He concluded that the 2 forms were interbreeding, and therefore could not be considered as separate species by a strict interpretation of the Biological Species Concept (Mayr 1942:120): "Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups." He relegated *caurina* to subspecies status within *americana*, and this usage has been followed since.

However, such a strict interpretation of species has been criticized as typological (Sokal and Crovello 1970), if it is taken to mean that even a single instance of hybridization in a single location is sufficient to invalidate the species distinction among all other populations everywhere else. Among other considerations, such a criterion does not consider the long-term biological consequences for the parent species, such as whether or not hybridization leads to reciprocal or unidirectional gene flow. If F_1 hybrids are uniformly sterile, for example, no genetic exchange can take place and the 2 lineages will maintain their separate evolutionary identities and histories, as required of good "evolutionary" species (Wiley 1981). Here, the mtDNA genetic evidence allows identification of the *caurina* and *americana* groups as distinct maternal lineages, which may therefore be considered good "phylogenetic" species: "[C]luster[s] of organisms, diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent." (Cracraft 1989:34-35). There are many examples in the literature of closely related species of mammals that have been shown to hybridize either in the wild or in captivity, yet which have retained their status as "good" species (Gray 1971). For example, North American white-tailed and mule deer (*Odocoileus virginianus* and *O. hemionus*, respectively) sometimes

hybridize in areas of sympatry (Carr et al. 1986). Both degree and direction of genetic introgression vary widely across the species' ranges, yet both species are readily distinguished morphologically and remain ecologically distinct (Carr and Hughes 1993, Hughes and Carr 1993). Among mustelids, sympatric Siberian populations of *M. martes* and *M. zibellina* are said to hybridize in the wild, producing a morphological intermediate known as a "kidus" (plural, "kiduses") (Grakov 1994), yet their status as separate species has in general not been questioned.

The morphological distinction between marten populations that are hereinafter referred to as *M. americana* and *M. caurina* are well documented (Hagmeier 1955, 1961; Anderson 1970). Even in Wright's (1953) original data, if the small number of martens with intermediate morphology are excluded, the remaining populations on either side of the species' boundary are readily distinguishable (Hicks 1996). A genetic examination of Wright's original material, now made possible by direct amplification of DNA from study skins (Hicks and Carr 1992), would permit a determination of the origin of the morphologically intermediate individuals.

The relationship of these data to the biogeography of North American martens has been considered previously (Hicks and Carr 1995). *M. caurina* was apparently confined to multiple glacial refugia in the west and southwest, in contrast to a single refugium for *M. americana* in the east (Graham and Graham 1994). The greater degree of genotypic diversity within *M. caurina* supports this theory. Preliminary genetic analysis of individuals representing the southernmost subspecies, *M. caurina sierrae*, indicates that although it is cladistically related to other *M. caurina* subspecies, it is a unique lineage in consequence of several distinct nucleotide substitutions. Re-analysis of the contemporary geographic distribution of martens seems to indicate that the *sierrae* and *humboldtensis* subspecies are disjunct from the other, more northerly subspecies of *M. caurina* (Graham and Graham 1994, cf. Hall 1981) (*humboldtensis* may now be virtually extinct: Zielinski et al., this volume). This disjunct distribution suggests that *sierrae* may have been confined to a separate glacial refugium, which may have persisted through several glacial cycles. Additional data on the genetic relationships of these subspecies are needed.

The genetic data also indicate that *M. pennanti* and *M. americana*/*M. caurina* represent separate invasions of the New World. The observed sequence differences between fisher and American marten genotypes range from about 12%-13% (Table 2). Given a molecular clock for this region of cytochrome *b* with a divergence rate of 2.5% per million years per pair of lineages (Carr and Hughes 1993), this rate implies a divergence at about 5 mybp. The first North American fisher, *M. diluviana*, appears in the early Pleistocene (1.8 mybp). This appearance indicates that the entry of the fisher occurred well after the establishment of the *Pekania* lineage in the eastern Palearctic. On the other hand, the sequence differences

among genotypes in *M. americana* and *M. caurina* are much smaller, ranging from 1.5%-2.0%, implying a separation at somewhat less than 1 mybp. The first fossil appearance of a true marten in North America, the noble marten (*M. nobilis*), during the late Pleistocene is consistent with this date. Youngman and Schueler (1991) have recently suggested that the noble marten is a subspecies of the *caurina* clade. If so, the implication of the genetic analysis is that the noble marten should be named *Martes caurina nobilis* (Hall 1926). Clarification of genetic relationships among extant subspecies of *M. caurina* may help to resolve the affinities and nomenclature of this fossil form.

Acknowledgments

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Appendix: Phylogenetic and Biogeographic Relationships of Subgenera *Martes*, *Charronia*, and *Pekania*

After completion of the above analysis, the senior author had the opportunity to review the genetic study of Hosoda et al. (this volume). Their data included homologous 401-base pair cytochrome *b* sequences from additional specimens of *M. melampus*, *M. zibellina*, and *M. americana*, as well as from the third subgenus (*Charronia*) of *Martes*, the yellow-throated marten (*M. flavigula*) from southeast Asia. With the kind permission of these colleagues, we combined our data sets and repeated the phylogenetic analysis of genus *Martes*. To determine the branching order of the 3 subgenera, we included as well data from 2 non-*Martes* species as outgroups, the North American badger (*Taxidea taxus*) (cf. Hicks and Carr 1995) and wolverine (*Gulo gulo*). Parsimony and bootstrap analyses were performed as previously described, except that transversion mutations (interchanges of purine for pyrimidine bases, or *vice versa*) were weighted 10:1 with respect to transitions (interchanges of purines, or of pyrimidines) to allow for the large genetic differences among genera.

The analysis identified 3 minimum-length trees (length 360) that differed only with respect to the exact relationships of TNP, SEL, and Hosoda et al.'s "Mam" genotype. Figure 3 shows the estimated branch lengths and bootstrap values for all branches supported in more than 50% of replications. Each of the 3 subgenera of *Martes* is monophyletic: subgenus *Charronia* (= *M. flavigula*) is the sister group to subgenus *Martes* in 66% of bootstrap replications, and subgenus *Pekania* (= *M. pennanti*) is the outgroup to the other 2 subgenera. Subgenus *Martes* is well-defined (occurrence in 91% of bootstrap replications). In this analysis, the Japanese *M. melampus* is grouped with the North American rather than the palearctic forms (cf. Fig. 2, and Hosoda et al., this volume), but bootstrap support for this arrangement is only 58%. Hosoda et al.'s American marten is from Maine, and is grouped with the eastern *M. americana* group, as predicted biogeographically. All specimens of *M. zibellina* are closely related. In this analysis, *Gulo* is the sister group to *Martes*, and *Taxidea* is the sister to *Gulo* and *Martes*. However, this arrangement is variable depending on the exact weighting scheme for transversions versus transitions, and further clarification of the branching order of these 3 genera is needed.

This analysis may help to clarify the biogeographic origins of *Martes* and its subgenera (cf. Hosoda et al., this volume). The maximum observed sequence difference within *Martes* (*sensu lato*) is ca. 12%-13% between *M. pennanti* and various *Martes* (*sensu stricto*) species (Table 2). As noted above, a molecular clock rate of 2.5% per million years per pair of lineages implies an initial divergence within the genus at about 5 mybp. This timing corresponds well to the first appearance of *M. paleosinensis* in the early Pliocene (4.8 mybp) of China. This

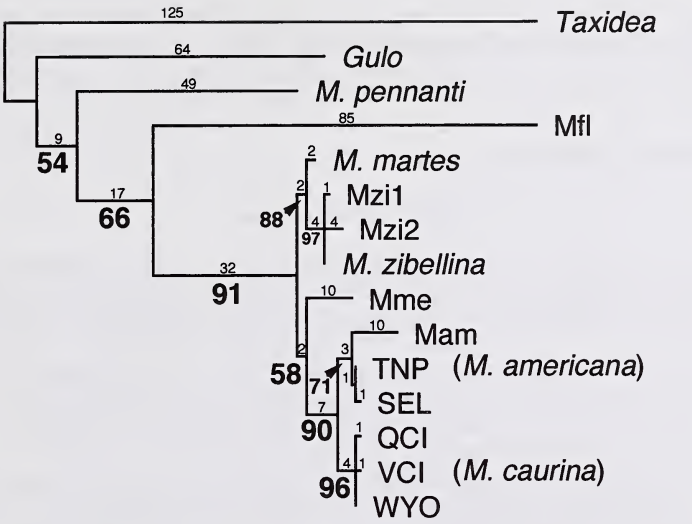

Figure 3. Phylogenetic tree (maximum parsimony) of mutational differences (transversions weighted 10:1 with respect to transitions) among mitochondrial cytochrome *b* genotypes in *Martes* spp. Species identifications are as in Figure 2, and in addition Mam, Mzi, Mme, and Mfl refer to sequences of *M. americana*, *M. zibellina* (2 specimens), *M. melampus*, and *M. flavigula* from Hosoda et al. (this volume). These data are used with their permission. The tree is rooted with respect to the genotype of *Taxidea*. Numbers above each branch indicate the inferred number of nucleotide substitutions that occur on that branch (transversions weighted as above). Numbers in bold below each branch indicate the percent occurrence of that group in 1000 bootstrap replicates.

species, like *M. pennanti*, has an external median rootlet on the fourth premolar and is therefore included in the subgenus *Pekania* (Anderson 1994). This dental character is absent from both *Charronia* and *Martes* subgenera, and can be regarded as a synapomorphy of *Pekania*. *M. lydekkeri* from the Pliocene of India is included in *Charronia* on biogeographic grounds (Anderson 1994); Hosoda et al. (this volume) estimated sequence divergences between *M. flavigula* and subgenus *Martes* that are consistent with this date. Thus, the genetic data clearly indicate that *"Martes" laevidens* from the early Miocene (ca. 19 mybp) of Europe, which has been included in the subgenus *Martes* (Anderson 1970, 1994),

is not in fact a member of the marten clade. Morphological affinities of *laevidens* and true martens should be re-evaluated. The branching order proposed here also suggests that the trend toward decreasing size seen from palearctic to nearctic *Martes* species (*sensu stricto*) is a continuation of a similar evolutionary trend from *Pekania* to *Charronia* to *Martes*, and can be understood as successive apomorphic transformations.

Note Added in Proof

Dr. Angus Davison (Univ. of Nottingham) kindly provided the senior author with the sequence of the western European beech or stone marten (*M. foina*). Inclusion of this sequence in the analysis described in the Appendix indicates that *M. foina* is the sister species to the remaining taxa of the subgenus *Martes*. *M. foina* forms a clade with the rest of the subgenus in 82% of bootstrap replications; the remaining taxa of the subgenus form a clade with *M. foina* as sister species in 93% of replications. This placement supports the conclusion of Anderson (1970, 1994), based on similarities of the dentition, that *M. foina* is closely related to the early middle Pleistocene species *M. vetus*, and represents an independent evolutionary lineage apart from the remaining species of the subgenus (cf. Anderson 1994: Fig. 1.1).

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GEOGRAPHIC VARIATION OF AMERICAN MARTEN IN CENTRAL AND NORTHERN QUEBEC

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Abstract: American marten (*Martes americana*) carcasses were collected from Cree and Innu trappers in 5 trapping divisions in central and northern Quebec during 4 trapping seasons (1989-1993). Fourteen cranial measurements of a sample of 1000 skulls were analyzed using Student's *t*-tests and indicated statistical differences ($P < 0.001$) for 9 measurements between populations in northern Quebec and populations of *M. a. americana* from Maine and New Brunswick . Mandible length, bimolar breadth, length of M_1 and condylobasal length showed the greatest differences. Geographic variation was also demonstrated between martens from the southern portion of our study area and those from the northern divisions.

Introduction

With the exception of Anticosti Island where it is now extinct (Newsom 1937), the American marten (*Martes americana*) is present in all forested regions of the province of Quebec (Anderson 1970, Banfield 1974, Strickland and Douglas 1987, Gibilisco 1994). It has been separated into 2 subspecies: *M. a. americana* which inhabits the southern part of the province, and *M. a. atrata* (Banfield 1974) or *M. a. brumalis* (Hall 1981) in the north. Both subspecies are present in our study area. Hagmeier (1961) separated American marten into 2 subspecies groups (*caurina* and *americana*) and found geographic variation in the *americana* group to be discordant. He also suggested that the 4 holarctic martens could be conspecific. Giannico and Nagorsen (1989) and Nagorsen (1994), using cranial measurements and body weight, respectively, found size and sexual dimorphism to be greater in insular populations of American marten.

The main objectives of our study, which was conducted within the framework of an ecological survey, were to assess geographic variation in American marten in central and northern Quebec and to compare our data with those from populations in the southern portion of the species' range in eastern North America.

Study Area and Methods

The study area includes 5 trapping divisions that cover more than 1,000,000 km^2 in central and northern Quebec (Fig.1). This territory is governed by the James Bay and Northern Quebec Convention, which guarantees exclusive trapping rights to Native peoples. This predominantly wilderness area is part of the Laurentian Precambrian shield and includes 3 bioclimatic zones (Payette 1983). The boreal zone situated between the 49th and 52nd parallels is characterized by black spruce (*Picea mariana*) stands, white birch (*Betula papyrifera*) and balsam fir (*Abies balsamea*). Low-density black spruce stands are present in the subarctic zone but are replaced by shrubs in the arctic zone where vegetation is very scarce. Annual snowfall averages 200 cm in Kuujjuak (trapping division 82) and 300 cm in Shefferville (division 82), Chibougamau (just south of division 56) and Matagami (division 58). Mean daily temperatures are 11°C and 12°C in July at Kuujjuak and Shefferville, respectively, and 16°C at Chibougamau. Mean daily temperatures for January are -23°C at Shefferville and Kuujjuak, and -18°C at Chibougamau.

Selected trappers in the 5 trapping divisions were given a $10 (CAN) incentive for each carcass remitted. Carcasses were collected from the fall of 1989 to the spring of 1993 (n = 1934) (Brunelle et al. 1991, Maltais et al. 1994). All specimens were sexed anatomically, and juveniles and adults were identified from radiographs of root canals of lower canines (Dix and Strickland 1986, Fortin et al. 1988). Bayes's law was used to calculate the probability of assigning an individual of unknown sex and age selected at random to the correct sex and age (Remington and Schork 1970). The age structure of the harvest was determined from reading cementum annuli of a random subsample of the adult segment of the 4-year harvest (n = 484) (Matson's laboratory, Milltown, Montana).

Fourteen cranial measurements were taken on a sample of 1000 skulls following the methods of Anderson (1970) (except for occipital height and auditory bulla width which were not measured by Anderson) to assess geographic variation among trapping divisions. The measurements were zygomatic breadth (ZB), interorbital breadth (INB), postorbital constriction (POC), bimolar breadth (WP^4-P^4), length of M_1 (LM_1), condylobasal length (CBL), palatal length (PL), maxillary tooth row length (LC-M^1), mandibular tooth row length (LC-M_2), mandible length (ML), rostral breadth (WC-C), cranial height (CH), occipital height (OH: from the dorsal margin of the foramen magnum to the top of the

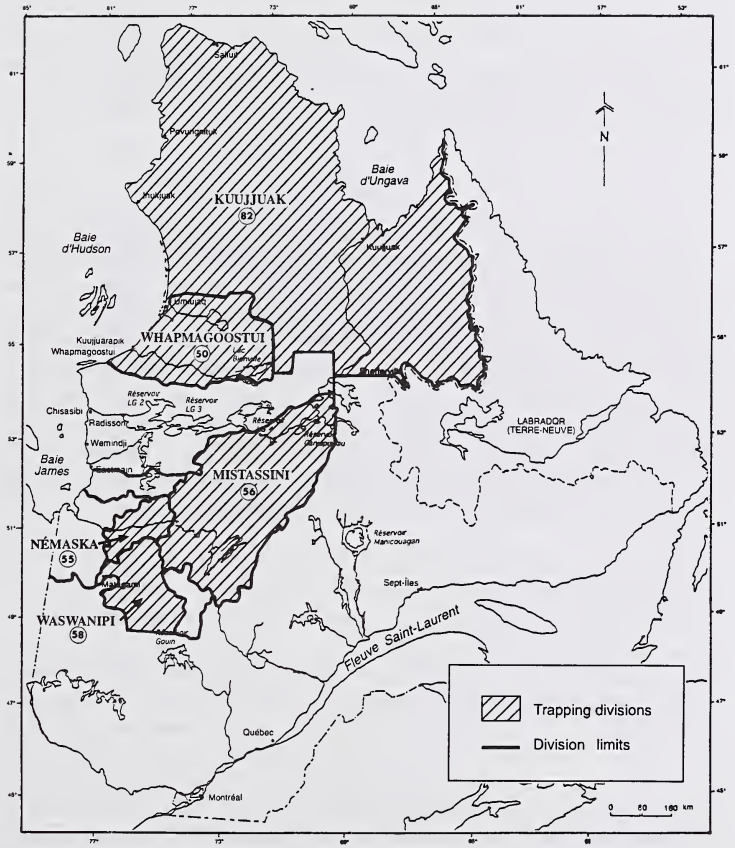

Figure 1. Map of Quebec, showing the locations of the 5 trapping divisions that comprised the study area.

skull), and auditory bulla width (ABW: from the external auditory meatus to the medial margin of the bulla). Data were analyzed using SAS/STAT (SAS 1988). Student's *t*-test was used to compare our data with those of Anderson (1970), who reported cranial dimensions of a sample of specimens of *Martes americana* from New Brunswick, and Soutiere (1985), who took similar measurements in Maine. Geographic variation among trapping divisions was investigated using discriminant analysis with 2 classification factors (sex and age) (Hair et al. 1987). Analysis of variance (ANOVA) was used to test for differences between adult males and females from our southern divisions and those from Maine and New Brunswick (Sokal and Rohlf 1981).

Results

Nine cranial measurements of American marten from Quebec (all divisions pooled) were significantly different from those reported by Anderson (1970) in New Brunswick and Soutiere (1985) in Maine (*t*-test, $P < 0.05$; Table 1). Seven of the cranial measurements from Quebec were larger than those of Anderson (1970) and Soutiere (1985) (ZB, INB, POC, WP^4-P^4, LM_1, CBL and PL), whereas the values of LC-M^1 and LC-M_2 were smaller than those reported by Anderson (1970) and Soutiere (1985). Those latter populations were both referred to *Martes americana americana* (Banfield 1974). Using ANOVA to compare adult specimens from the southern portion of our study area (Fig. 1: divisions 55, 56, 58) to those from New Brunswick and Maine, we obtained the same results with a higher level of significance ($P < 0.001$; exception, female POC, $P = 0.005$; Table 2).

Thirteen of the 14 variables (exception: PL) were used to investigate geographic variation within Quebec. Discriminant analysis with 2 classification factors (sex and age) indicated that adult males ($n = 172$), juvenile males ($n = 197$), adult females ($n = 132$) and juvenile females ($n = 136$) belong to 4 statistically different groups ($P < 0.01$). The 2 discriminant functions accounted for 89.7% and 59.4% of the total variance in adult males and juvenile males, whereas they accounted for 88.5% and 66.6% in adult females and juvenile females, respectively (Table 3). Graphic representation of the centroids and their confidence limits ($P < 0.05$) of each group for all trapping divisions illustrates the differences among divisions and the relationship between divisions 50 and 82 in the northern portion of the study area, and divisions 55, 56 and 58 in the south (Fig. 2). Based on the Student's *t*-test, adult specimens from the southern and northern divisions differ significantly in cranial size ($P < 0.00001$; exception, female POC, $P = 0.005$; Table 4). Based on this series of 13 cranial measures, American marten from the northern divisions have larger skulls than those from the southern divisions.

Table 1. Cranial dimensions (mm) of American martens from different localities in North America.

		Quebec[a]			New Brunswick			Maine		
	Sex	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*
ZB	male	45.00	3.08	441	42.34	3.05	25	42.81	1.71	79
	female	40.50	1.62	318	37.38	1.56	21	37.81	1.91	16
INB	male	18.17	1.14	427	16.91	0.82	17	16.83	0.68	81
	female	16.55	1.02	321	15.22	0.71	16	15.39	0.98	17
POC	male	16.46	1.21	425	15.37	0.64	17	14.54	1.18	82
	female	15.28	1.09	321	14.97	1.04	16	14.55	0.73	17
WP^4- P^4	male	24.78	1.17	450	23.58	0.75	17	22.39	0.84	82
	female	22.63	0.99	326	21.68	0.54	15	20.73	1.62	17
LM_1	male	8.92	0.46	458	7.91	0.19	21	8.01	0.40	80
	female	8.04	0.41	334	7.30	0.36	18	7.13	0.59	17
CBL	male	82.08	3.23	451	76.64	1.82	27	75.50	1.58	80
	female	74.49	2.90	324	69.01	2.47	21	69.24	2.62	17
PL	male	41.00	2.93	453	37.68	1.68	16	37.22	1.08	83
	female	36.44	2.12	329	33.71	1.29	16	33.58	1.71	17
LC-M^1	male	23.47	1.01	447	27.64	0.96	27	26.06	0.73	83
	female	21.16	0.97	324	24.79	0.89	23	23.79	1.11	17
LC-M_2	male	29.26	1.13	448	32.61	0.94	25	30.83	0.77	80
	female	26.28	1.03	324	29.25	0.91	22	28.05	1.51	17

[a] All measurements from Quebec differ significantly ($P < 0.05$) from those from New Brunswick and Maine.

Discussion

On the basis of color and size, Bangs (1898) classified American marten from the Quebec-Labrador peninsula north of Mistassini lake as *Martes americana brumalis*. Despite differences between the northern Quebec and Newfoundland populations reported by Hagmeier (1958), Hagmeier (1961), who measured 107 specimens of *brumalis* and 11 specimens of *atrata* from Newfoundland, argued that these populations were "identical." Nonetheless, Hall (1981) listed them as

Table 2. Cranial dimensions of adult American martens from central Quebec and other localities in North America.

		Quebec[a] Divisions 55, 56, 58			New Brunswick			Maine					
	Sex	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*	df1	df2	*F*
ZB	male	46.55	2.01	114	42.34	3.05	25	42.81	1.71	79	2	215	94.75
	female	40.46	1.62	84	37.38	1.56	21	37.81	1.91	16	2	118	39.13
INB	male	18.31	0.83	109	16.91	0.82	17	16.83	0.68	81	2	204	93.62
	female	16.54	0.79	82	15.22	0.71	16	15.39	0.98	17	2	112	27.79
POC	male	15.43	1.01	110	15.37	0.64	17	14.54	1.18	82	2	206	17.40
	female	15.28	1.17	82	14.97	1.04	16	14.55	0.73	17	2	112	3.29
WP^4- P^4	male	24.60	0.81	113	23.58	0.75	17	22.39	0.84	82	2	209	175.51
	female	22.33	0.85	82	21.68	0.54	16	20.73	1.62	17	2	111	20.25
LM_1	male	8.87	0.38	115	7.91	0.19	21	8.01	0.40	80	2	213	166.22
	female	8.00	0.37	85	7.30	0.36	18	7.13	0.59	17	2	117	53.46
CBL	male	81.36	2.39	113	76.64	1.82	27	75.50	1.58	80	2	217	202.31
	female	73.90	2.53	83	69.01	2.47	21	69.24	2.62	17	2	118	45.75
PL	male	40.31	1.35	64	37.68	1.68	16	37.22	1.08	83	2	160	111.48
	female	36.17	1.51	84	33.71	1.29	16	33.58	1.71	17	2	114	32.44
LC-M^1	male	23.33	0.83	110	27.64	0.96	27	26.06	0.73	83	2	217	449.91
	female	21.07	0.88	82	24.79	0.89	23	23.79	1.11	17	2	119	178.73
LC-M_2	male	28.97	0.91	110	32.61	0.94	25	30.83	0.77	80	2	212	228.96
	female	26.09	1.01	83	29.25	0.91	22	28.05	1.51	17	2	119	84.48

[a] All values from Quebec differ significantly ($P < 0.001$) from those from New Brunswick and Maine, except for female POC ($P > 0.05$).

Table 3. Standardized coefficients of the first 2 discriminant functions for sex and age groups of American martens from Quebec.

Character	Adult males		Juvenile males		Adult females		Juvenile females	
	DF1	DF2	DF1	DF2	DF1	DF2	DF1	DF2
ZB	-0.039	-0.023	0.090	-0.006	0.035	0.046	0.130	-0.047
WC-C	0.011	0.092	-0.021	-0.026	0.009	-0.011	0.035	0.005
INB	0.023	0.028	0.004	-0.090	0.010	-0.024	-0.009	-0.039
POC	0.014	-0.024	0.021	0.079	-0.028	0.132	0.010	0.092
WP^4-P^4	0.023	-0.068	-0.017	0.002	0.041	-0.020	0.005	0.008
ML	0.057	-0.016	-0.018	-0.001	-0.000	0.051	-0.072	0.116
LM_1	0.026	0.065	0.025	-0.004	-0.009	0.011	-0.008	-0.036
CBL	0.031	-0.056	0.037	-0.046	0.045	0.025	-0.047	-0.016
CH	0.032	0.030	0.013	0.050	0.041	-0.110	-0.041	-0.047
OH	0.034	-0.025	0.036	0.048	0.036	0.021	0.026	0.039
ABW	-0.028	0.045	0.036	-0.008	-0.004	-0.013	-0.036	0.000
LC-M^1	-0.009	0.071	0.003	-0.046	0.015	-0.092	0.038	0.056
LC-M_2	-0.048	-0.085	-0.064	0.088	-0.094	0.070	0.059	-0.050
% variance	66.0	23.3	44.7	19.6	62.7	27.8	43.7	20.5

distinct subspecies. American marten from trapping divisions 50 and 82 in northern Quebec have much larger skulls and differ in other cranial morphometrics from specimens studied by Anderson (1970) and Soutiere (1985) from southern populations referred to *M. a. americana*. Mean dimensions of 5 cranial characters (CBL, INB, WC-C, WP^4-P^4, LM_1) from a pooled sample from divisions 50 and 82 fall within the range of measurements listed by Anderson (1970) for *M. a. brumalis* (her $n = 5$).

These results are consistent with subspecific separation of marten in the northern trapping divisions from *M. a. americana,* but cannot address the suggested synonymy of *M. a. brumalis* with *M. a. atrata*. Taxonomic conclusions must await more detailed studies of geographic variation in the *americana* group that consider both morphological and genetic characters. Specimens from the southern

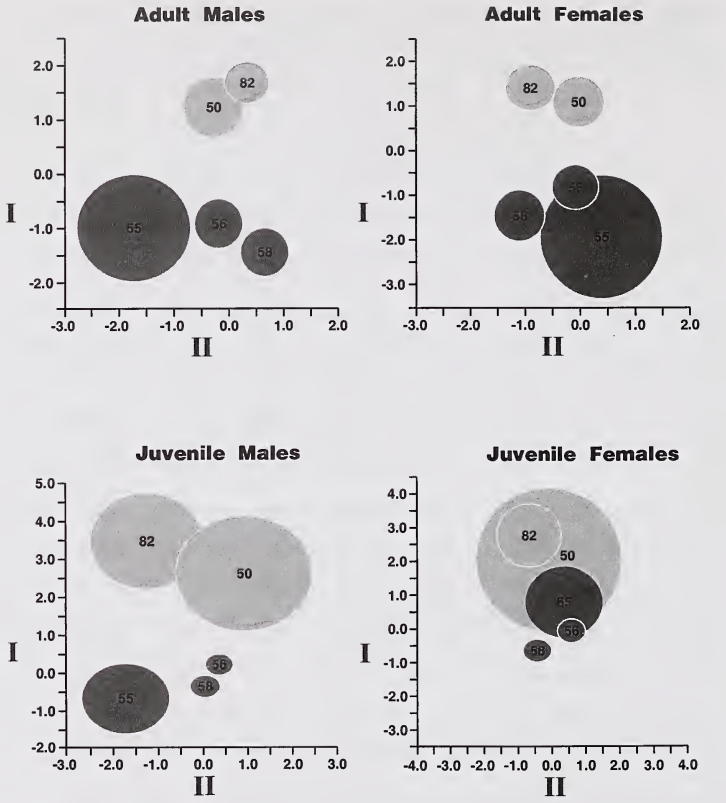

Figure 2. Discriminant analysis based on sex and age. Centroids and their confidence limits ($P < 0.05$) of the 4 population segments for all trapping divisions.

portion of our study area have smaller skulls than those from the northern divisions, but larger skulls from the southern populations fall within the range of specimens from the north. Specimens referable to *M. a. americana* may be present in the southern sample. Caution must be exercised in classifying individual martens from the southern portion of our study area to subspecies because the location of contact with *M. a. americana* is unknown. Geographical variation in the skull size of American marten was also noted by Hagmeier (1961) for the *caurina* group on the Pacific coast. Our data confirm the existence of a population

Table 4. Cranial dimensions of adult American martens from central and northern Quebec.

		Divisions 50 and 82			Divisions 55, 56, 58			
	Sex	Mean	SD	*n*	Mean	SD	*n*	*t*
ZB	male	48.65	2.04	92	46.55	2.01	114	7.42
	female	43.19	1.31	78	40.46	1.62	84	11.75
WC-C	male	16.55	0.66	97	15.49	0.72	115	11.13
	female	14.67	0.51	84	13.69	0.72	85	10.23
INB	male	19.43	0.79	92	18.31	0.83	109	9.79
	female	17.64	0.68	81	16.54	0.79	82	9.51
POC	male	16.43	1.10	93	15.43	1.01	110	6.70
	female	15.73	1.01	82	15.28	1.17	82	2.60
WP^4- P^4	male	26.04	0.88	96	26.60	0.81	113	12.26
	female	23.64	0.68	85	22.33	0.85	82	11.03
ML	male	57.49	1.91	94	54.35	1.69	115	12.56
	female	50.29	1.67	83	48.02	1.86	84	8.29
LM_1	male	9.32	0.34	97	8.87	0.38	115	8.94
	female	8.35	0.32	86	8.00	0.37	85	6.73
CBL	male	85.61	2.48	96	81.36	2.39	113	12.58
	female	77.13	2.22	82	73.90	2.53	83	8.69
CH	male	31.89	1.11	97	30.11	1.17	115	11.24
	female	29.30	0.98	84	27.87	1.14	83	8.69
OH	male	17.24	1.19	93	15.88	1.16	110	8.23
	female	13.97	0.88	83	12.75	0.93	82	8.68
ABW	male	10.85	0.56	97	10.38	0.56	115	6.10
	female	10.14	0.45	86	9.68	0.47	84	6.40
LC-M^1	male	24.43	0.84	95	23.33	0.83	110	9.44
	female	22.02	0.76	81	21.07	0.88	82	7.33
LC-M_2	male	30.23	0.92	95	28.97	0.91	110	9.84
	female	27.04	0.81	79	26.09	1.01	83	6.57

of American martens of large size in northern Quebec that shows some geographical variation, possibly due to environmental factors. Future research in eastern North America should include studies on the geographical variation in American marten throughout its range.

Acknowledgments

We acknowledge the participation of all Cree and Innu trappers who turned in their marten carcasses and the staff of the Nouveau-Québec region of the Ministère de l'Environnement et de la Faune who collected the biological material. We thank the Société d'énergie de la Baie James that funded the project and Yves Garant of Laval University.

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SKELETAL MORPHOMETRICS OF FISHERS FROM ALBERTA: SEXUAL SIZE DIMORPHISM AND AGE-CLASS COMPARISONS

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Abstract: Differences in size between sexes and between juvenile (<1 year of age) and adult age classes of fisher (*Martes pennanti*) from Alberta were investigated using a morphometric analysis of the skeleton (9 cranial, 3 dental, and 6 postcranial characters). Based on an overall measure of skull size, juvenile males were 16% larger than juvenile females, whereas adult males were 19% larger than adult females. Differences in size between age classes were small in both sexes. Males demonstrated more significant differences ($P < 0.05$) between age classes in individual skull measurements than females; this result suggests that females reach their maximum body size at a younger age than males. Among the 6 appendicular long bones, ranges of greatest lengths in males and females overlapped only for the ulna and femur, in which the overlap was small. In both sexes, differences in limb bone lengths between age classes were not significant. In a principal components analysis of the pooled sample, 91% of the total variation was attributed to differences in size; each measurement contributed more-or-less equally to the size axis. Principal component analyses for each sex demonstrated significant size- and shape-related differences among individuals. There was no correlation ($P > 0.05$) between skull or limb bone measurements and geographic location, as measured along either a latitudinal or longitudinal axis. Based on preliminary comparisons of condylobasal skull lengths, fishers from Alberta are larger than those in reported samples representing the 3 currently recognized subspecies of *M. pennanti*. Nonetheless, differences in size among these samples are small, suggesting that the recognition of subspecies based on size-related criteria may be suspect.

Introduction

The fisher (*Martes pennanti*) is found throughout the boreal forest of North America (Powell 1981, 1982). Previous studies of the qualitative and quantitative morphology of the skeleton of the fisher (e.g., Leach and Dagg 1976, Leach 1977, Leach and de Kleer 1978) were based on specimens from the eastern portion of the species' range. No study has examined a large sample of fishers from Alberta. Of the 321 specimens studied by Hagmeier (1959) in his re-evaluation of the validity of subspecies of *Martes pennanti*, only 5 came from Alberta. The lack of comparative data on specimens from Alberta is probably the result of the historical paucity of skeletal material from this province in museum collections.

In 1990 the Provincial Museum of Alberta (PMA) acquired 114 fisher carcasses from throughout the Alberta range of the species. This acquisition provided the opportunity for morphometric analyses based on a reasonably large and representative sample of fishers from the province. Using mensural data, and other information associated with each specimen (sex, age, collecting locality), we addressed the following: (1) variation in cranial and postcranial measurements associated with age (adult versus juvenile) and sex, (2) variation in size associated with geographic location (latitude and longitude), and (3) the implications of these data for Hagmeier's (1959) conclusions regarding the subspecific taxonomy of the Alberta population.

Materials and Methods

Specimen Acquisition

In the fall of 1989, the Alberta Department of Forestry, Lands, and Wildlife (Fish and Wildlife Division) made a request to trappers that fisher carcasses be turned in to local Fish and Wildlife officers; 103 of the 114 specimens collected were included in this study. The study sample included specimens from throughout the Alberta range of the species but representation by region was uneven. Thirty percent of the sample came from northeastern Alberta between 55° and 56° N latitude and between 110° and 114° W longitude (see Appendix). The northernmost and westernmost portions of the province were poorly represented (Fig. 1).

Adults (>1 year of age) were distinguished from juveniles by the ratio of the width of the pulp cavity to that of the crown of the upper canine, a measurement that accurately separates adult and juvenile age classes of fisher (Jenks et al. 1984, Dix and Strickland 1986). Sex was determined by the presence or absence of a baculum and was confirmed during specimen preparation. Geographic location was known for 92 specimens (Fig. 1; Appendix). Given that animals were collected between November 1989 and January 1990, and assuming that birth

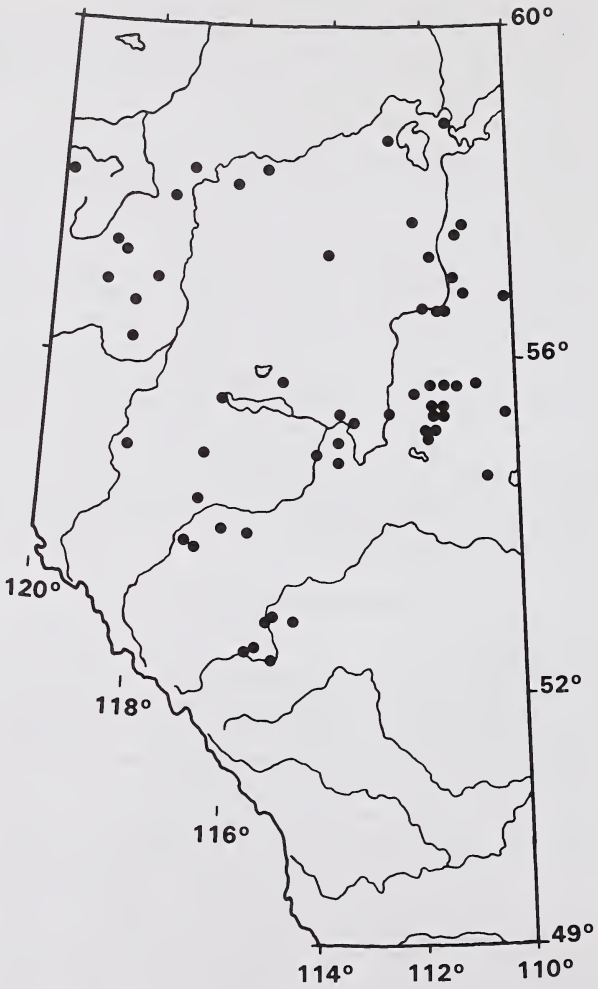

Figure 1. Map of Alberta showing the trapping location of 92 fisher specimens. Some locations provided more than 1 specimen.

occurs between February and May (Powell 1981), the age of juveniles in the sample was between 6 and 11 months, whereas adults were at least 18 months of age. Thus, animals aged 11 to 18 months are not represented by this sample.

Collection of Morphometric Data

Measurements were taken with electronic calipers to the nearest 0.01 mm. Most cranial measurements followed Hagmeier (1959) and included condylobasal length, palate length, palate width at P2, upper tooth row length, length of the fourth upper premolar, upper molar width, bulla length, canine width, rostrum width, preorbital width, zygomatic width, and mastoid width (Fig. 2). Using the sum of all cranial and dental measurements, an overall "skull size" character was calculated. A sum of morphometric characters provides an idealized size measurement equivalent (except for scaling) to a principal component axis with a uniform eigenvector (McGillivray and Johnston 1987); this measurement was used in analyses that required an index of overall size. However, skull size could be determined only for those specimens with a complete set of

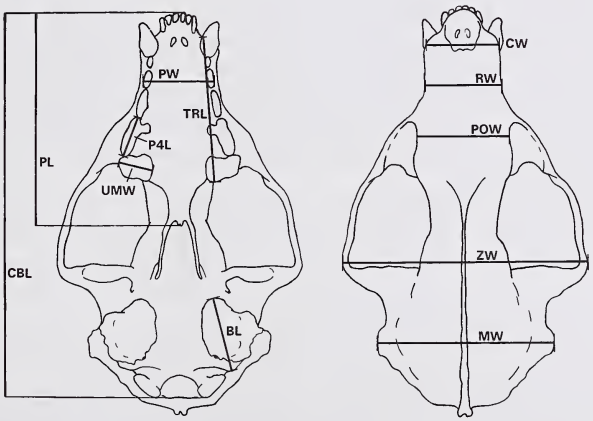

Figure 2. Skull of the fisher in ventral (left) and dorsal (right) views showing the cranial and dental measurements used in this analysis. Abbreviations: BL, bulla length; CBL, condylobasal length; CW, canine width; MW, mastoid width; P4L, fourth premolar length; PL, palate length; POW, preorbital width; PW, palate width; RW, rostrum width; UMW, upper molar width; TRL, upper tooth row length; ZW, zygomatic width.

measurements. Because some skulls had sustained damage during collection, sample sizes for the skull size variable were reduced. The greatest length of each long bone (humerus, ulna, radius, femur, tibia, fibula) was also measured. Long bones from the same limb were measured wherever possible.

Seventeen percent of the total sample was remeasured to assess measurement error. The percentage error in the measurement of a particular variable (j) is:

$$\frac{\Sigma_{i=1}^{n} (X_{ij1} - X_{ij2})/((X_{ij1} + X_{ij2})/2) \times 100\%}{n}$$

where X_{ij1} is the first and X_{ij2} the second measurement of variable j on specimen i, and n is the number of specimens. Measurement errors ranged from 0.07% to 1.54%. Most measurements showed high repeatability; only 2 had errors greater than 1% (rostrum width, 1.25%; palate width, 1.54%). Interpretation of statistical tests involving these 2 variables must consider this level of measurement error.

Data Analysis

Data were analyzed using univariate and multivariate statistical methods in the SAS computer package (SAS Institute 1985). Means and standard errors were calculated for each measurement. Because there are only 2 sexes and 2 age classes, differences between variable means were assessed univariately with *t*-tests. Simultaneous assessment of age- and sex-related differences is possible using ANOVA, but we did not have a balanced design and were interested in evaluating the affect of each factor separately. Ranges were determined for limb bone measurements.

Principal component analysis (PCA), using a correlation matrix, was used to determine the major sources of variation in the data. PCA using a correlation matrix was chosen to minimize the effect of unequal variable variances on the interpretation of the axes (McGillivray 1985). Analyses were run on each sex separately and on the combined sample.

Relationships between skull size and long bone lengths and both the latitude and longitude of the collecting locality were examined using correlation analysis. Eleven specimens had no locality data and were excluded from this analysis.

The results of this study were compared with those reported in previous papers on the osteology of fishers (e.g., Hagmeier 1959, Leach and Dagg 1976, Leach 1977). Mean condylobasal lengths of adult male and female fishers from this study were compared with values for the fisher subspecies reported by Hagmeier (1959). Means and standard errors for Hagmeier's samples were taken from Figure 2 in his paper.

Results

Fishers from Alberta show strong sexual size dimorphism with both juvenile and adult males being significantly larger than females (Tables 1 and 2, respectively). The skulls of the juvenile males were approximately 16% larger than those of juvenile females, whereas the skulls of adult males were approximately 19% larger than those of adult females. Differences in individual measurements between male and female juvenile fishers ranged from 9.0% (bulla length) to 23.3% (canine width, rostrum width). Differences in individual measurements

Table 1. Comparison of skeletal measurements in male and female juvenile fishers. Mean values (mm) ± standard error with sample size in parentheses, followed by percentage difference in males compared to females and the *t* value ($P < 0.0001$ in all cases).

Measurement	Males	Females	%	*t*
condylobasal length	117.57±0.46 (23)	101.67±0.30 (35)	15.6	30.52
palate length	64.67±0.35 (26)	54.73±0.20 (36)	18.2	24.89
palate width	20.11±0.14 (26)	17.53±0.09 (38)	14.7	16.50
upper tooth row length	43.74±0.19 (28)	38.08±0.11 (37)	14.9	25.69
fourth premolar length	12.45±0.06 (28)	10.83±0.05 (38)	15.0	21.04
upper molar width	10.97±0.07 (28)	9.48±0.05 (17)	15.7	17.87
bulla length	23.43±0.16 (27)	21.49±0.12 (37)	9.0	10.02
canine width	24.18±0.14 (26)	19.61±0.11 (37)	23.3	27.03
rostrum width	24.60±0.16 (26)	19.95±0.14 (37)	23.3	22.09
preorbital width	26.32±0.26 (25)	22.76±0.15 (32)	15.6	11.87
zygomatic width	65.98±0.59 (13)	56.60±0.33 (25)	16.6	15.04
mastoid width	55.21±0.29 (25)	46.81±0.15 (36)	17.9	25.81
skull	486.86±2.61 (11)	420.96±1.62 (20)	15.7	22.63
humerus length	98.98±0.51 (21)	86.41±0.30 (35)	14.5	22.86
ulna length	95.94±0.61 (19)	82.96±0.28 (34)	15.6	19.38
radius length	78.35±0.44 (22)	67.81±0.25 (35)	15.5	22.59
femur length	107.31±0.56 (22)	94.18±0.30 (36)	13.9	20.85
tibia length	112.79±0.67 (22)	98.69±0.36 (36)	14.3	20.29
fibula length	104.11±0.71 (18)	91.18±0.36 (35)	14.2	18.22

Table 2. Comparison of skeletal measurements in male and female adult fishers. Mean values (mm) ± standard error with sample size in parentheses, followed by percentage difference in males compared to females and the *t* value ($P < 0.0001$ in all cases).

Measurement	Males	Females	%	*t*
condylobasal length	119.30±0.63 (18)	102.74±0.69 (15)	16.1	17.78
palate length	65.76±0.51 (19)	55.54±0.42 (15)	18.4	14.89
palate width	20.87±0.16 (19)	17.94±0.19 (17)	16.3	11.92
upper tooth row length	44.45±0.29 (19)	38.71±0.30 (17)	14.8	13.88
fourth premolar length	12.55±0.09 (19)	10.97±0.08 (17)	14.4	13.45
upper molar width	11.24±0.10 (19)	9.51±0.09 (17)	18.2	12.84
bulla length	23.08±0.17 (18)	21.72±0.22 (15)	6.3	4.95
canine width	25.00±0.15 (18)	20.08±0.18 (16)	24.5	21.03
rostrum width	25.15±0.31 (19)	20.28±0.18 (16)	24.0	13.50
preorbital width	27.36±0.27 (16)	23.00±0.31 (15)	19.0	10.65
zygomatic width	75.80±0.63 (16)	58.80±0.47 (13)	28.9	20.78
mastoid width	56.75±0.32 (18)	47.40±0.26 (15)	19.7	21.98
skull	508.26±2.05 (13)	427.86±3.21 (12)	18.8	21.42
humerus length	99.36±0.58 (18)	86.51±0.51 (16)	14.9	16.53
ulna length	95.82±0.58 (18)	84.34±0.85 (13)	13.6	12.19
radius length	78.49±0.45 (18)	68.38±0.45 (14)	14.8	15.67
femur length	108.39±0.57 (17)	94.88±0.68 (16)	14.2	15.33
tibia length	113.77±0.69 (18)	99.47±0.88 (16)	14.4	12.94
fibula length	104.84±0.64 (18)	92.33±0.84 (16)	13.5	11.95

between male and female adult fishers ranged from 6.3% (bulla length) to 28.9% (zygomatic width).

In both sexes there were significant differences in skull size between juveniles and adults (Table 3). The adult males were significantly larger than the juvenile males in overall skull size and in 8 individual measurements (6 cranial, 2 dental), whereas the adult females were significantly larger than the juvenile females in overall skull size, but in only 4 individual cranial measurements (Table 3). In males the skull of adults was 4.4% larger than that of juveniles, whereas in females the skull of adults was 1.6% larger than that of juveniles. Because the

Table 3. Differences in skeletal measurements between juvenile and adult fishers based on the percentage difference in adults compared to juveniles for each sex (t values: * – $P < 0.05$; ** – $P < 0.001$; *** – $P < 0.0001$). See Tables 1 and 2 for mean values.

	Males		Females	
Measurement	%	t	%	t
condylobasal length	1.5	2.28*	1.1	1.69
palate length	1.7	1.82	1.5	2.01
palate width	3.8	3.59*	2.3	2.27*
upper tooth row length	1.6	2.13*	1.7	1.98
fourth premolar length	0.8	1.04	1.3	1.52
upper molar width	2.5	2.36*	0.9	1.00
bulla length	-1.5	-1.41	1.1	1.01
canine width	3.4	4.00*	2.4	2.32*
rostrum width	2.2	1.59	1.7	1.35
preorbital width	4.0	2.82*	1.1	0.78
zygomatic width	14.9	11.19***	3.9	3.85**
mastoid width	2.9	3.54*	1.3	2.06*
skull	4.4	6.53***	1.6	2.13*
humerus length	0.4	0.49	0.1	0.19
ulna length	-0.1	-0.16	1.7	1.54
radius length	0.2	0.22	0.8	1.18
femur length	1.0	1.33	0.8	0.96
tibia length	0.9	1.01	0.8	0.82
fibula length	0.7	0.76	1.3	1.26

Table 4. Ranges of lengths (mm) of long bones of male and female fishers from Alberta (* – no overlap in ranges).

Long bone	Females	Males
humerus	82.84 - 90.23	92.76 - 105.26 *
ulna	79.87 - 91.97	91.39 - 101.16
radius	64.04 - 71.47	73.83 - 83.01 *
femur	90.10 - 100.49	100.23 - 114.08
tibia	90.63 - 104.74	105.50 - 121.03 *
fibula	83.45 - 96.60	98.78 - 111.74 *

measurement error for palate width was 1.54%, the validity of significant age-related differences in this character must be considered suspect. In both sexes there were no significant differences in long bone lengths between juveniles and adults (Table 3). This result indicates that in both sexes the postcranial body size of juveniles approaches that of adults. There was little or no overlap in the ranges of limb bone lengths in male and female fishers (Table 4). A small overlap in these ranges occurred in the ulna and femur.

When all specimens were pooled, the first principal component (PC 1) of the PCA accounted for 90.8% of the total variation and was the only significant axis. The elements of the first eigenvector (Table 5) were all positive and nearly equal; hence PC 1 can be interpreted as a size axis (Somers 1986). When males and females were analyzed separately, 4 significant principal components were extracted from the male sample and 3 were extracted from the female sample (Table 6). Eigenvectors of only PC 1 and PC 2 are readily interpretable. Eigenvectors for PC 1 suggest that it can be interpreted as a size axis in both sexes. PC 2 showed a contrast between skull and long bone measurements in both sexes (Table 7). Individuals with relatively large skulls and short long bones scored higher on this axis.

No significant correlations ($P > 0.05$) were found between skull size or limb bone lengths and either the latitude or longitude of the collecting locality in both males and females.

The mean condylobasal length of both male and female adult fishers from Alberta was greater than lengths from any of the subspecific samples of Hagmeier (1959); lengths for *Martes pennanti columbiana* most closely approach the means for the Alberta sample (Table 8). Because Hagmeier (1959) separated adults and juveniles on a different criterion (fusion of the nasomaxillary sutures) from that used in this study, statistical comparison of sample means was inappropriate.

Table 5. Eigenvector of principal component 1 for skeletal measurements of male and female fishers from Alberta.

Measurement	Eigenvector (PC 1)
condylobasal length	0.245
palate length	0.244
palate width	0.222
upper tooth row length	0.240
fourth premolar length	0.235
upper molar length	0.237
bulla length	0.202
canine width	0.243
rostrum width	0.229
preorbital width	0.230
zygomatic width	0.228
mastoid width	0.240
humerus length	0.237
ulna length	0.242
radius length	0.241
femur length	0.240
tibia length	0.241
fibula length	0.241

Discussion

A high degree of sexual size dimorphism has been reported in other fisher populations (e.g., Hagmeier 1959, Leach and Dagg 1976, Leach 1977, Leach and de Kleer 1978, Powell 1982, Holmes and Powell 1994). In comparisons of body weight in fisher populations from across North America (Powell 1982: Table 1), males weighed from 64% to 124% more than females. Sexual size dimorphism

Table 6. Eigenvalues for the 4 significant principal components based on separate samples of male and female fishers from Alberta. The proportion of the variance explained by each component is given as a percent in parentheses.

Principal component	Males	Females
1	9.06 (50.3)	10.86 (60.3)
2	3.21 (17.8)	2.23 (12.4)
3	1.61 (8.9)	1.46 (8.1)
4	1.23 (6.8)	0.88 (4.9)

in the condylobasal length of the skull in the Alberta population is similar to that found by Hagmeier (1959, adult males 17% larger than adult females). The extreme sexual dimorphism in the width across the zygomatic arches in adults (28.9%) is indicative of a marked difference between the sexes in the volume of the jaw musculature. Because the temporalis musculature passes medially to the arch and inserts on the coronoid process of the lower jaw, the volume of this muscle affects the position of the arch. Differences in muscle size are also reflected in the development of the sagittal crest, which is extremely pronounced, especially posteriorly, in older adult males (see Wright and Coulter 1967). The degree of dimorphism is similar in the skull and the postcranial skeleton (Tables 1, 2). This result does not agree with Holmes and Powell's (1994) conclusion that mustelines show less dimorphism in the skull than in overall body size. The small overlap in the range of the lengths of the long bones in males and females is similar to that reported by Leach and Dagg (1976) and Leach (1977), who found an overlap in ranges only for the femur in fishers from Ontario. The significant dimorphism in juveniles, which are at least 6 months old, is consistent with evidence that the size of male and female siblings is the same up to an age of 4 months (Douglas and Strickland 1987), but that sexual dimorphism in weight is evident by 5 months of age (Powell 1982).

The larger number of significant differences in the size of skull measurements between juvenile and adult males, as compared to juvenile and adult females, indicates that the skull of juvenile females is closer to adult size than is that of the juvenile males and is associated with differences in growth trajectories between the sexes. This result is consistent with a study of fishers from Maine in which all cranial sutures of juvenile males were open, whereas many were partially fused in juvenile females (Wright and Coulter 1967). The large difference

Table 7. Eigenvectors of the first 2 principal components based on separate samples of males and females.

	Males		Females	
Measurement	PC 1	PC 2	PC 1	PC 2
condylobasal length.	0.284	0.067	0.280	-0.034
palate length	0.320	0.037	0.258	-0.052
palate width	0.120	0.410	0.147	0.448
upper tooth row length	0.260	0.296	0.228	-0.050
fourth premolar length	0.113	0.446	0.194	0.058
upper molar width	0.175	0.144	0.182	0.172
bulla length	0.065	-0.068	0.188	0.211
canine width	0.276	0.206	0.243	0.308
rostrum width	0.184	0.136	0.207	0.323
preorbital width	0.249	0.147	0.185	0.266
zygomatic width	0.235	0.167	0.225	0.310
mastoid width	0.214	0.017	0.262	0.008
humerus length	0.170	-0.347	0.251	-0.255
ulna length	0.284	-0.231	0.263	-0.264
radius length	0.268	-0.232	0.253	-0.295
femur length	0.242	-0.308	0.267	-0.184
tibia length	0.293	-0.224	0.281	-0.206
fibula length	0.298	-0.194	0.271	-0.227

in zygomatic width between juvenile and adult males indicates that much of the growth of the jaw musculature occurs after the first year; in females the age-related difference in this variable is only slightly larger than that in other cranial measurements. Female fishers reach adult weight in 5.5 to 6 months, whereas males may take more than a year to reach maximum weight (Powell 1981). As the age of juvenile animals in this study is estimated at between 6 and 11 months, juvenile females should have reached adult size whereas the males have not. The absence of significant differences in long bone lengths between juveniles and adults in both sexes is consistent with observations that, even in males, the degree of

Table 8. Comparison of condylobasal length in adult fishers from Alberta with those of the subspecific samples of Hagmeier (1959). Values are means (mm) ± standard errors with sample sizes in parentheses.

Subspecies	Males	Females
Alberta sample	119.30 ± 0.63 (18)	102.74 ± 0.69 (15)
M. p. pennanti	115.2 ± 0.7 (12)	97.8 ± 0.7 (17)
"intergrades"	116.9 ± 0.5 (15)	100.1 ± 0.4 (17)
M. p. columbiana	117.9 ± 0.5 (33)	100.4 ± 0.3 (35)
M. p. pacifica	114.2 ± 0.5 (24)	99.9 ± 0.6 (10)

fusion of the distal epiphysis of the femur cannot reliably separate juveniles and adults (Dagg et al. 1975), and the body length of juveniles approaches that of adults by 5 months (Douglas and Strickland 1987). Nonetheless, epiphyseal fusion of the long bones occurs later in males (Dagg et al. 1975, Douglas and Strickland 1987). In both sexes the long bones reach adult size before the skull is fully grown. Similarly, in the American marten (*Martes americana*) epiphyseal fusion in the long bones precedes closure of many of the cranial sutures (Strickland and Douglas 1987).

The main source of variation among individuals is size as indicated by the large percentage of the total variance that is explained by PC 1. However, there are intrasexual differences in shape as evidenced by the significance of PC 2 in both sexes. Although it is not unequivocally an age axis, PC 2 nonetheless separates individuals by the relative size of the skull, as compared to that of the long bones. Juveniles, with their relatively small skulls but adult-sized long bones, scored relatively low on this axis. Thus, the PCA supports the results of the univariate analysis that suggested differential growth rates in the skull and long bones in both sexes. The attainment of adult body size in the long bones by 6 to 11 months of age may be important for the dispersal of juveniles that occurs in the fall; juveniles may travel extensively during their first year (Arthur et al. 1989).

Two major hypotheses have been proposed to explain sexual size dimorphism in mustelids (Moors 1980, Holmes and Powell 1994). In the first, dimorphism is viewed as a mechanism to reduce competition between the sexes, allowing males and females to exploit prey of different sizes (Brown and Lasiewski 1972). However, Giuliano et al. (1989) found no evidence for resource partitioning by sex in fishers, and Holmes and Powell (1994) did not find the geographic variation in the degree of sexual dimorphism in *Martes* that is predicted by this hypothesis. The second hypothesis states that sexual size dimorphism results from different selective pressures that influence size independently in each sex (Erlinge

1979, Moors 1980, Holmes and Powell 1994). In mammalian carnivorans this mechanism is correlated with extreme polygyny and a minimal parental investment by males (Ralls 1976). Although there is support for this hypothesis in mustelines such as *Martes* and *Mustela* spp. (Erlinge 1979, Powell 1979, Moors 1980, Powell and Leonard 1983), and specifically in the fisher (Powell 1979, Powell and Leonard 1983), evidence that male fishers may be territorial to reduce competition for food, rather than for mates (Arthur et al. 1989), may be inconsistent with this second hypothesis.

Suggested explanations for the occurrence of sexual size dimorphism in mustelids are often at least implicitly, and sometimes explicitly, specific for particular genera or species (e.g., Brown and Lasiewski 1972, Erlinge 1979, Wiig 1986). However, sexual dimorphism in body size is characteristic of the Mustelidae (Moors 1980). Sexual size dimorphism is especially evident in the Mustelinae (Holmes and Powell 1994), but is less pronounced among mephitines (Van Gelder 1968), and in populations of species of the otter *Lontra* (1% - 12%; van Zyll de Jong 1972) and the badger *Meles* (1%, Hysing-Dahl 1954, cited by Wiig 1986). Given that the Mustelidae is a clade (Wozencraft 1989, Bryant et al. 1993, Wyss and Flynn 1993), the occurrence of sexual size dimorphism in extant mustelids is associated with phylogenetic history. Mustelines, and *Martes* in particular, appear to be close to the base of the modern mustelid radiation (Bryant et al. 1993), suggesting that pronounced sexual size dimorphism is probably plesiomorphic for the extant Mustelidae and occurs in these taxa as a result of inheritance from the common ancestor of the clade. If the occurrence of this dimorphism is the result of history, separate adaptation-based explanations for sexual size dimorphism in each musteline genus or species are inappropriate. Species-specific arguments must focus instead on the degree of dimorphism. There also appears to be an inverse correlation between the degree of dimorphism and male weight (Moors 1980); fishers appear to be highly dimorphic for their size. This observation suggests that analyses of sexual dimorphism in fishers should concentrate on attempts to explain why it is relatively high in this species.

The absence of a significant correlation between latitude and skull and long bone size suggests that variation in size in fishers in Alberta does not follow Bergmann's rule. However, Bergmann's rule may not be applicable to mammal populations in Alberta because there is no direct correlation between latitude and ambient temperatures in the province because of the influence of the Rocky Mountains (McGillivray 1985).

Goldman (1935) recognized 3 subspecies of *Martes pennanti* based on differences in condylobasal length and proportions of the skull. Since then, populations in eastern North America extending west to the Ontario/Manitoba border have been referred to *M. p. pennanti*, those in the Rocky Mountains and west to the coast ranges have been referred to *M. p. columbiana*, and populations in the

Coast Mountains, Cascade Range, and Sierra Nevadas have been referred to *M. p. pacifica*. Populations in Manitoba, Saskatchewan and Alberta have been referred to *M. p. columbiana* (Goldman 1935), divided between *M. p. columbiana* and *M. p. pennanti* with northern populations being assigned to the former (Hall and Kelson 1959, Hall 1981), or referred to an intergrade population between typical *M. p. pennanti* in the east and typical *M. p. columbiana* in the Rocky Mountains (Hagmeier 1959). Thus, the Alberta population has been referred either to *M. p. columbiana* (Goldman 1935, Soper 1964, Hall 1981) or to an intergrade population (Hagmeier 1959). In contrast, Banfield (1974) did not recognize subspecies of *M. pennanti*.

Hagmeier (1959) concluded that condylobasal length increases from that in the eastern populations referred to *Martes pennanti pennanti* to that in the mountain subspecies *M. p. columbiana* and then declines in the west coast populations referred to *M. p. pacifica*. Mean condylobasal lengths of adult males and females in the present sample are slightly less than those of the topotypes (5 males, 5 females) of *M. p. columbiana* from Stuart Lake, British Columbia (Goldman 1935). Based on the skull sizes in Hagmeier's (1959) larger samples of the 3 subspecies, the present sample from Alberta would be referred to *M. p. columbiana* (Table 8). In contrast, Hagmeier (1959) referred the Alberta population to the intergrade group. Although Hagmeier (1959) considered the intergrade group to be intermediate in size between typical *M. p. pennanti* and *M. p. columbiana*, mean condylobasal length of the present sample from Alberta is greater than that of Hagmeier's sample of the latter subspecies. However, his sample of males from Alberta consisted of only 2 specimens, which had a mean condylobasal length that was greater than the mean for *M. p. columbiana*. Thus, the mean skull length in the Alberta population to the east of the mountains may be larger than lengths in the other documented populations of the species.

Hagmeier (1959) argued that differences in body size among North American fishers are minor and clinal. He concluded that there was little value in recognizing subspecies of *Martes pennanti* but did not formally change the subspecific taxonomy. Certainly the demarcation of subspecies based on body size will be arbitrary (Anderson 1970). Youngman (1975) noted that differences between eastern and northwestern populations were well below levels conventionally used for recognizing subspecies based on size. The question of subspecies in fishers should be addressed using multivariate and genetic techniques.

Whether or not variation in size is indicative of subspecific differentiation, there is solid evidence for geographic variation in size in the fisher (Hagmeier 1959). Existing data do not provide insight into the source of this variation. Interspecific competition has been suggested as an explanation for variation in size among populations of American marten in British Columbia (Giannico and Nagorsen 1989, Nagorsen 1994). In fisher, historical factors, current ecological conditions,

and varying degrees of interspecific and sexual selection may all contribute to the differences in body size.

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Appendix

Table 9. Locality (latitude and longitude) of origin of fishers from Alberta examined in this study.

Location	Males		Females		Total
	Juveniles	Adults	Juveniles	Adults	
52°-53°N; 114°-116°W			3	3	6
53°-54°N; 114°-116°W			1		1
53°-54°N; 116°-118°W	1		1	1	3
54°-55°N; 112°-114°W	1				1
54°-55°N; 114°-116°W	1	1			2
54°-55°N; 116°-118°W	1	1	1		3
54°-55°N; 118°-120°W				1	1
55°-56°N; 110°-112°W	6	5	9	3	23
55°-56°N; 112°-114°W	3	1	2	3	9
55°-56°N; 114°-116°W	1				1
55°-56°N; 116°-118°W		1			1
56°-57°N; 110°-112°W	2	2	2		6
56°-57°N; 112°-114°W	3				3
56°-57°N; 116°-118°W			1		1
56°-57°N; 118°-120°W	1	1	3		5
57°-58°N; 110°-112°W	1	1	7	1	10
57°-58°N; 112°-114°W		1			1
57°-58°N; 114°-116°W	2		1		3
57°-58°N; 116°-118°W		1			1
57°-58°N; 118°-120°W			1	1	2
58°-59°N; 110°-112°W			1	1	2
58°-59°N; 112°-114°W		1	1	1	3
58°-59°N; 114°-116°W	1				1
58°-59°N; 116°-118°W			1	1	2
58°-59°N; 118°-120°W				1	1
Location unknown	4	3	4		11
Total	28	19	39	17	103

Part II

Population Ecology and Behavior

Martes: taxonomy, ecology, techniques, and management, pages 61-77.
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AGE, SEX STRUCTURE, AND FECUNDITY OF THE AMERICAN MARTEN IN MONTANA

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Abstract: Age and sex structure of the American marten (*Martes americana*) in Montana was determined from 2521 skulls collected from trappers between 1987 and 1993. Age was determined from radiographs and cementum annuli. Fecundity and ovulation rates were determined by examining 383 female reproductive tracts. Corpora lutea were counted in hand-sectioned and histologically prepared ovary pairs. The mean number of corpora lutea found in ovaries of ovulating females was 2.6 (SD = 0.8, $n = 225$). The mean number of corpora lutea found in northwestern Montana martens (3.2) was significantly different ($P < 0.05$) from those from southwestern Montana (2.5). Fewer 1.5 year-old females (85.5%) ovulated than females over 2.5 years of age (95.5%). The ratio of males per female in annual harvests ranged from 1.0 to 1.5. The proportion of juveniles in the annual harvest varied from 33.2 to 63.7%. Juveniles per adult female ≥2.5 yrs ranged from 2.6 to 8.7 during the 5 winters. The number of juveniles per adult female ≥1.5 yrs ranged from 1.1 to 4.2. The mean age of martens harvested was 1.6 yrs (SD = 0.3, $n = 2399$). A decline in the number of juveniles in the harvest occurred throughout Montana in 1992-93. The proportion of males in the harvest declined from 1989 to 1993. Annual age distributions, and possible causes for variations in data between years and geographic regions of Montana, are discussed.

Introduction

The American marten (*Martes americana*) is widely distributed throughout the vast and often remote areas of central and western Montana (Gibilisco 1994). Due to its secretive nature, it is difficult and prohibitively expensive for wildlife managers to directly monitor populations. Direct population measures are also difficult to obtain throughout most portions of the geographic range of the American marten. Because of these logistic restrictions and the subsequent economic costs of population monitoring, wildlife managers throughout North America face a significant challenge in responsibly managing American marten populations and regulating the harvest.

Indirect measures of population change such as fluctuations in age and sex structure, harvests or fecundity are often used to infer population trends (Strickland and Douglas 1987, Fortin and Cantin 1994, Mead 1994, Strickland 1994). The differences in vulnerability between males and females, and between juveniles and adults, have been used to develop indices of harvest intensity (Strickland and Douglas 1987). Previous population studies showed that heavy trapping tends to selectively remove old animals and skews age structure toward young animals (Strickland and Douglas 1987, Fortin and Cantin 1994). Other studies indicated that when the sex ratio of the harvest has a greater number of females than males, overharvest is likely (Soukkala 1983, Fortin and Cantin 1994). Strickland (1994) suggested 3 age and sex ratio indices for monitoring harvest intensity: the number of juveniles/mother, the number of juveniles/female and the ratio of males to females. Although corpora lutea counts accurately reflect ovulation rates but do not accurately indicate litter size (Mead 1994), they are used to measure fecundity in marten populations. Strickland et al. (1982) reported that an acceptable harvest rate is indicated by a juvenile/mother ratio greater than the fecundity, and a juvenile/female ratio ≥ 3. In this study we monitored changes in age structure, sex structure and fecundity of marten populations trapped from two distinct regions of Montana in order to compare harvest programs within two significantly different habitats.

Study Area

The study area encompassed the portions of Montana where American martens are harvested. The state is divided into 7 administrative regions (Fig. 1). American martens are harvested in 5 of these regions. However, the vast majority of marten are harvested in administrative regions 1 (Northwest Region), 2 (West-central Region), and 3 (Southwest Region).

In the Northwest Region, marten habitat extends continuously across the landscape ranging from low forested valley bottoms to alpine elevations. Valley base elevations range from 700 to 1200 m and valley floors are commonly forested (Pfister et al. 1977). The major mountain ranges rise to elevations of 2100-2800 m and support forested habitats up to alpine levels. Valley forest types include *Thuja*, *Picea*, and *Tsuga* habitats. Mountain forests are dominated by *Abies* and *Pseudotsuga* habitats. Climate is characterized by a strong maritime influence with an annual mean temperature of 6.5°C (US Department of Commerce NOAA 1994). Precipitation is distributed evenly throughout the year and averages 50 cm annually.

In southwestern Montana, marten habitats occur in high elevation mountain ranges that are interrupted by large open grassland valleys, resulting in naturally fragmented habitats isolating populations of marten (Gibilisco 1994). Forested

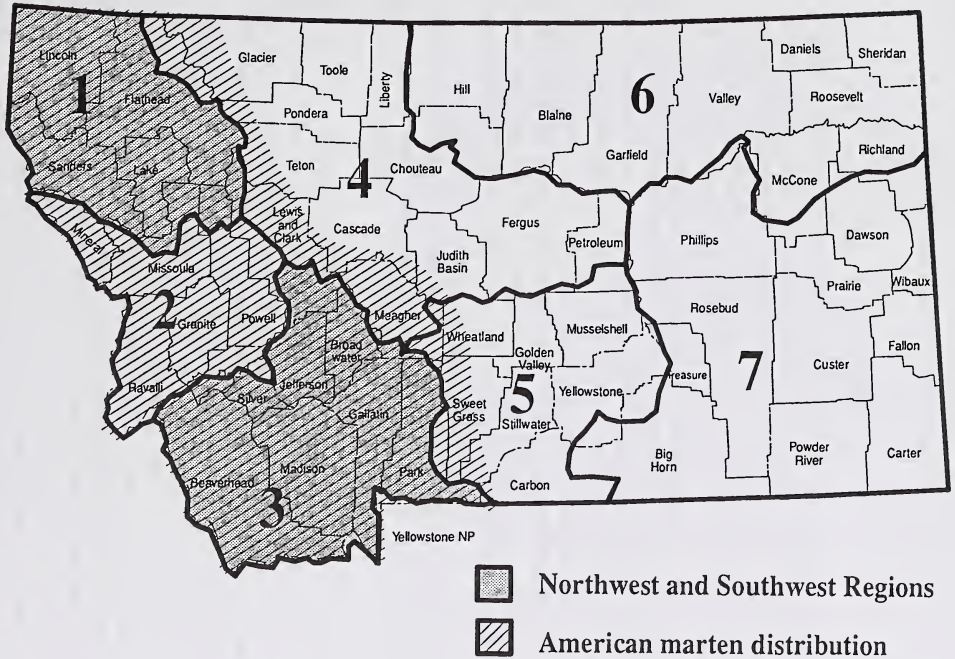

Figure 1. Administrative regions and the distribution of the American marten in Montana.

mountain habitats range from 1500 to 2800 m in elevation. Mountain forest types consist predominantly of *Pinus contorta, Pseudotsuga menziesii, and Pinus albicaulis* (Pfister et al. 1977). Climate is characterized by a strong continental influence and average annual temperature is 5°C (US Department of Commerce NOAA 1994). Precipitation is seasonal and averages 40 cm annually.

Methods

Montana trappers in the Southwest Region voluntarily provided marten carcasses from the 1987-88 through 1993-94 trapping seasons. Statewide collections were initiated for 1989-90 and continued through the 1993-94 trapping season. Montana trappers were notified of the voluntary carcass program through the annual season regulation pamphlet and by verbal contact by regional field personnel. Carcasses were frozen in the field by each trapper and transported to 1 of 5 regional offices, where they were stored in freezers until delivery to the Montana Fish, Wildlife and Parks (MFWP) Wildlife Laboratory for examination.

Trappers also provided annual harvest data by submitting each marten pelt for tagging and registration as required by regulation during the annual furbearer season. Annual harvest data reported in a statewide fur survey and inventory were used to evaluate success of the volunteer carcass collection efforts. We considered the voluntary collections to be adequate if they resulted in a sample of 30% or more of the total harvest registered for each region.

At the MFWP Wildlife Laboratory marten carcasses were sexed and weighed then dissected to extract reproductive and gastro-intestinal tracts. Reproductive tracts were fixed in 10% formalin. Stomach and colon contents were extracted, washed, and frozen.

An upper canine tooth was extracted from each skull after gentle warming at 80°C for approximately 30 min. All canines were placed on a gridded cardboard sheet and radiographed to identify juveniles (Dix and Strickland 1986, Nagorsen et al. 1988). Canine pulp cavity measurements were made under magnification. We established a pulp cavity to tooth width ratio of greater than 35% for classifying juveniles, by comparing pulp cavity measurements of 744 martens that were radiographed and aged by cementum annuli at Matson's Laboratory (Milltown, Montana). Four hundred and eighteen of 424 (98.6%) juvenile martens were correctly classified using this criterion. For all martens with a pulp cavity of 35% or less, the root tip was removed with a dremel tool and submitted to Matson's laboratory for cementum analysis. Juvenile age determinations based on cementum analysis were further evaluated based on morphological characteristics of the reproductive tract and the presence/absence of corpora lutea. We assumed that juvenile martens could not be reproductively active; therefore, if corpora lutea were detected, that marten's age was adjusted upward one age class (Poole et al. 1994).

Ovaries were collected between the winter of 1987-88 through that of 1991-92. Each ovary was excised from its reproductive tract and weighed. Ovaries collected from 1987-88 through 1989-90 were hand-sectioned into 1 mm slices to count corpora lutea, whereas those collected during 1990-91 and 1991-92 winters were histologically sectioned, stained with hematoxylin-eosin, and examined with a compound light microscope (Wright 1963). Sixteen ovary pairs were examined macroscopically and microscopically in 1990 to determine if macroscopic counts underestimated corpora lutea counts.

The fixed uterus was processed according to Mead (1994). The length of each uterine horn was measured and the uterus was placed in 70% alcohol for a minimum of 24 hrs. The uterus was then dried in 95% alcohol and cleared in methyl salicylate (Mead 1994). Cleared tracts were examined with a dissecting scope and substage mirror to identify placental scars.

Comparisons of mean counts of corpora lutea and age ratios from different geographic regions were made using the Mann-Whitney test. Analysis of variance was used to compare ovulation rates among age groups or years. The hypothesis that there are no differences in ovulation rate between geographic regions or between yearlings and adults was tested using chi-square statistics.

We calculated the ratio of juveniles/mother, juveniles/adult female and male/female according to Strickland (1994). This author defined mothers as female martens aged 2.5 yrs and older, whereas adult females are aged 1.5 yrs and older. Mean fecundity was determined according to methods outlined in Strickland and Douglas (1987). Mean fecundity is defined as the product of percent females ovulating and mean corpora lutea per ovulating female divided by 100.

Results

Carcass Collections and Annual Harvest

Annual harvests of American marten declined in all regions of Montana from 1987-88 to 1993-94 (Fig. 2). The average harvest from 1987-88 to 1993-94 was 1192.7 (SD = 577.2, n = 7). The average annual harvest in the Northwest and Southwest Regions during this period was 518 (SD = 165.2, n = 7) and 297 (SD = 214.4, n = 7), respectively.

We examined specimens from 42.3% of the statewide marten harvest. We received marten carcasses from 51.7% of the total harvest in the Southwest Region between 1987 and 1994, and 32.5% of the total in the Northwest Region during the sampling period of 1989-1994. Marten carcasses were regularly collected from the northwestern and southwestern regions of Montana. Other regions of the state participated intermittently, or provided a sample of marten carcasses representing less than 30% of the total harvest.

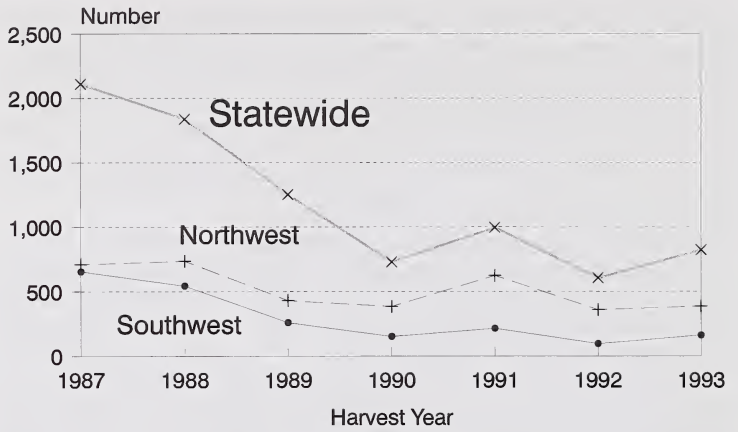

Figure 2. Trends in marten harvest, 1987-1993, in the Southwest and Northwest Regions of Montana, and statewide.

Age and Sex Structure

Sex Ratios: The male:female ratio for all years in the southwest, northwest and statewide was 1.2, 1.4, and 1.3, respectively. It remained stable from 1987 to 1991 and then began to shift towards parity in the 1992 and 1993 harvests (Fig. 3). In southwest Montana, sex ratios were not equal in the winters of 1988-89 and 1989-90 ($\chi^2 = 8.0$ and 4.0, respectively; df = 1; $P < 0.05$). In northwest Montana, sex ratios were not equal in all winters except 1993-94 ($\chi^2 = 8.5$, 4.2, 12.6, and 3.8, respectively; df = 1; $P < 0.05$). During the winter of 1993-94 sex ratios were equal in both regions ($\chi^2 = 0.04$ and 0.35, respectively; df = 1; $P = 0.8$ and 0.6, respectively).

Age Structure: The total sample of 2399 aged martens included 1011 females, 1334 males, and 54 animals of undetermined sex. The mean age of the male, female and total samples was 1.6 yrs (SD = 0.5, 0.5, and 0.3, respectively). The oldest-aged marten was 10 yrs in the southwest and 12 yrs in the northwest.

Age distribution curves for southwest Montana indicated that the years 1989-90 and 1992-93 were visibly different from other years (Fig. 4). The age distributions between years 1989-90 and 1992-93 in the southwestern region were not different from each other ($\chi^2 = 7.162$, df = 1, $P = 0.4127$). Comparisons of each of these 2 years to all other years indicated a significant difference between these distributions (Table 1). The major dissimilarity in the 1989-90 and 1992-93 distributions, as compared to other years, was the percent of juveniles in the harvest which declined to less than 50%.

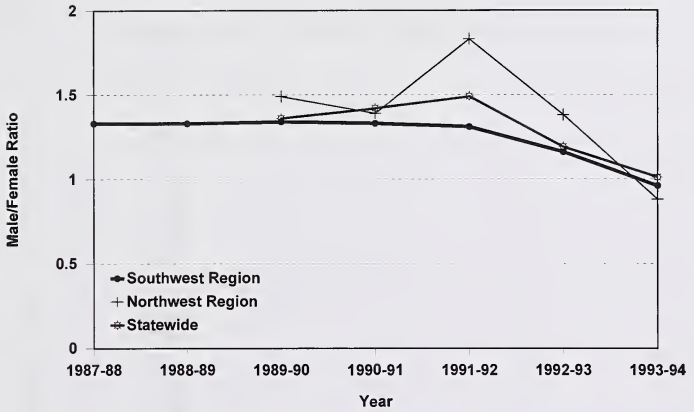

Figure 3. Sex ratios of marten harvests, 1987 to 1993, in the Southwest and Northwest Regions of Montana, and statewide.

In northwest Montana, the age distribution for 1992-93 was significantly different from those of other years (Table 1). The proportion of juveniles in the harvest declined to less than 50% and the proportion of 1 year-old martens increased to over 30% in that year (Fig. 5).

Age Ratios: The proportion of juveniles in the annual harvests fluctuated from 0.4 to 0.6 for the Southwest Region (Table 2). The proportion of juveniles in the harvests from the Northwest Region ranged from 0.3 and 0.7. There was no difference in the proportion of juveniles between Southwest and Northwest harvests ($Z = 0.97$, $P = 0.33$).

The ratio of juveniles/female ≥ 2.5 yrs ranged from 2.8 to 8.2 in southwestern Montana and from 2.6 to 8.7 in northwestern Montana (Table 2). We found no difference in ratios of juveniles/female ≥ 1.5 yrs ($Z = 0.49$, $P = 0.63$) or juveniles/female ≥ 2.5 yrs ($Z = 0.0$, $P = 1.0$) between the Southwest and Northwest Regions.

Reproduction and Fecundity

Morphology of Reproductive Tracts: In total, 383 reproductive tracts were extracted from female marten carcasses from 1987-1994. We found no difference in the mean length of right (39.8 mm) and left (39.3 mm) uterine horns ($t = 0.56$, df = 458, $P = 0.57$) or weight of right and left ovaries ($t = 1.18$, df = 334, $P = 0.23$). For subsequent age-related morphologic comparisons, we used data from the right uterine horn and ovary.

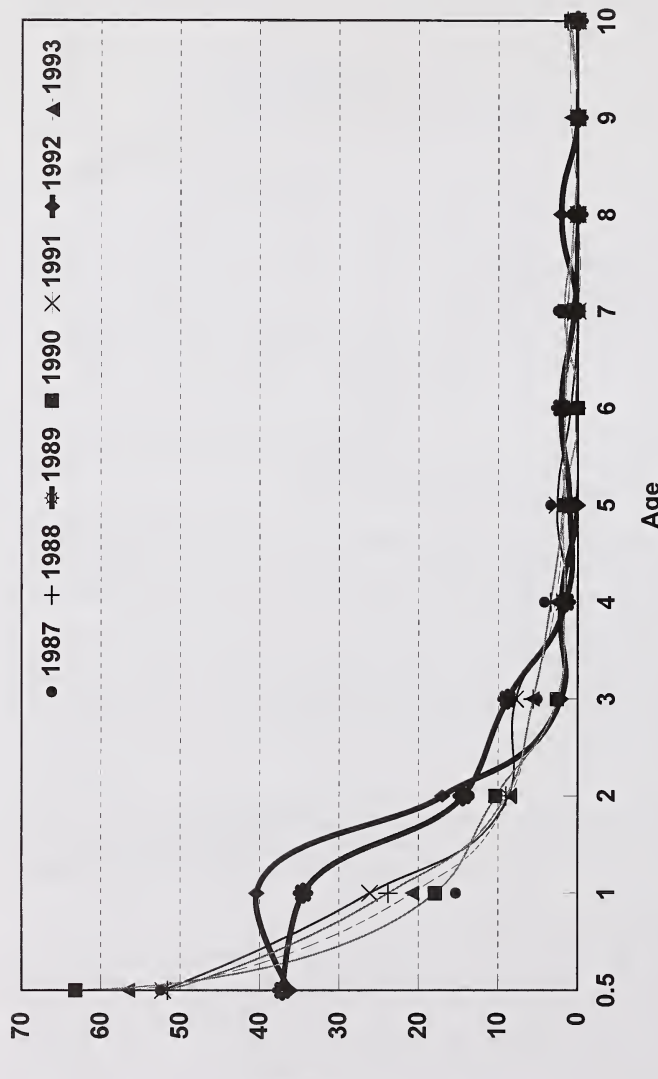

Figure 4. Age structure of American marten populations harvested in the Southwest Region of Montana, 1987-1993.

Table 1. Chi-square and *P* values for comparisons between annual age distributions of martens in northwest and southwest Montana, 1987-1993.

Year Compared	Northwest Region		Southwest Region	
	χ^2	*P*	χ^2	*P*
89-87	-	-	52.7	0.00
89-88	-	-	111.8	0.00
89-90	-	-	50.5	0.00
89-91	-	-	16.5	0.02
89-92	132.6	0.00	7.2	0.41
89-93	-	-	26.6	0.00
92-87	-	-	62.8	0.00
92-88	-	-	124.8	0.00
92-90	97.7	0.00	44.2	0.00
92-91	79.6	0.00	37.7	0.00
92-93	35.3	0.00	39.9	0.00

The mean length of the right uterine horn of juvenile martens (29.2 mm) was significantly less than that of adult martens (44.1 mm) ($t = 14.39$, df = 220, $P < 0.05$). The right uterine horn was significantly shorter in juvenile and yearling martens than in martens ≥ 2 yrs ($F = 49.212$, df = 221, $P < 0.05$; Table 3). Ovary weights increased until age 2 and mean weight of juvenile ovaries was significantly lower than that of other age classes ($F = 11.899$, df = 163, $P < 0.05$; Table 3).

Ovulation Rates: Ninety-three percent of 353 adult female martens had ovulated. The percent of yearlings that ovulated (85.5%, $n = 110$) was significantly lower than that of females ≥ 2.5 yrs (95.5%, $n = 243$) ($\chi^2 = 25.35$, df = 1, $P < 0.001$). Ovulation rates increased slightly until 3.5 yrs (Table 4).

Ovulation rates ranged from 76% to 95% in the Southwest Region between 1987-88 and 1991-92 (Table 5). The lowest ovulation rate (1991-92) was significantly different from the highest rates (1988-89 and 1989-90; $\chi^2 = 9.9$, df = 1, $P < 0.05$; $\chi^2 = 8.4$, df = 1, $P < 0.05$). There were no significant differences in ovulation rate between 1991-92, 1990-91, and 1987-88 ($\chi^2 = 1.87$, df = 1, $P = 0.17$; $\chi^2 = 2.36$, df = 1, $P = 0.12$).

Ovulation rates ranged from 81% to 93% in the Northwest Region between 1989-90 and 1991-92 (Table 5). We found no significant differences between the lowest of these three rates (1991-92) and those for the other two years (1990-91 and 1989-90; $\chi^2 = 1.88$, df = 1, $P = 0.17$; $\chi^2 = 1.21$, df = 1, $P = 0.27$).

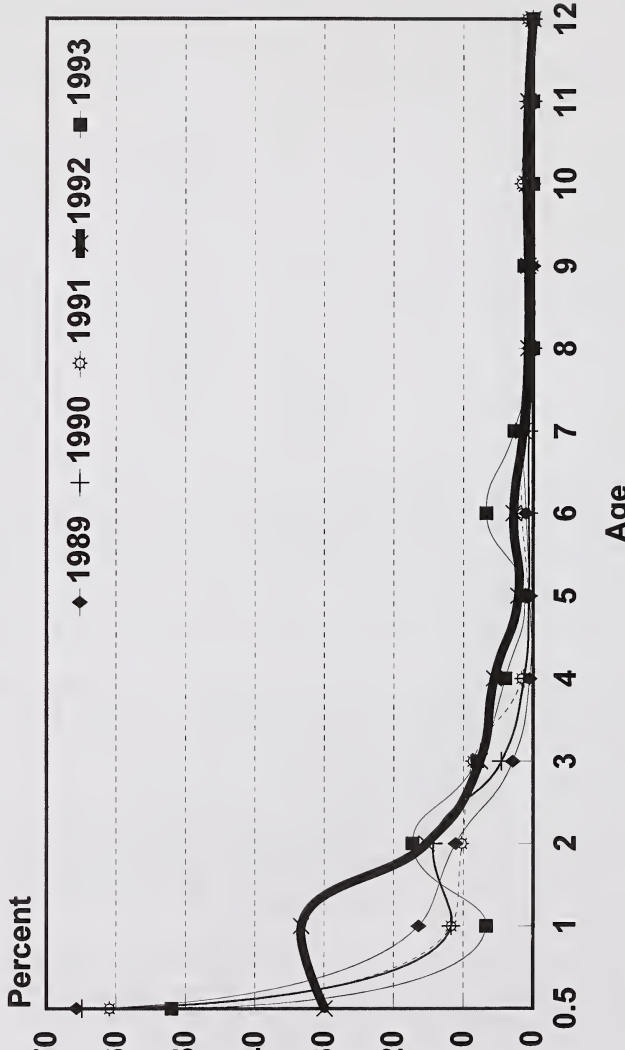

Figure 5. Age structure of American marten populations harvested in the Northwest Region of Montana, 1989-1993.

Table 2. Annual marten age ratios between 1987-1993 in the southwest, northwest, and the entire state of Montana.

	Proportion Juveniles			Juveniles/Adult Female ≥2.5 yrs			Juveniles/Adult Female ≥1.5 yrs		
Year	SW	NW	State	SW	NW	State	SW	NW	State
1987-88	0.517	-	-	3.81	-	-	2.54	-	-
1988-89	0.515	-		4.43	-	-	2.35	-	-
1989-90	0.371	0.657	0.529	2.77	8.50	5.80	1.47	5.04	2.77
1990-91	0.632	0.649	0.637	8.22	7.69	8.71	4.35	4.00	4.18
1991-92	0.522	0.609	0.588	6.00	6.00	5.53	2.73	4.11	3.42
1992-93	0.362	0.299	0.332	4.25	2.39	2.55	1.42	1.05	1.14
1993-94	0.566	0.520	0.539	6.66	2.60	3.97	3.16	2.17	2.57
Mean	0.497	0.546	0.525	5.16	5.44	5.31	2.57	3.27	2.82
SD	0.099	0.148	0.116	1.88	2.83	2.31	1.01	1.62	1.13

Corpora Lutea Counts and Fecundity: We found no difference in the mean number of corpora lutea in 16 ovary pairs examined macroscopically and microscopically ($t = 0.63$, df = 30, $P = 0.535$). The median count for each method was 3.

The mean number of corpora lutea in ovary pairs of females >1.5 yrs was 1.6 (SD = 0.7, $n = 383$). The number of corpora lutea in ovary pairs from ovulating females throughout Montana ranged from 1 to 6 and averaged 2.6 (SD = 0.8, $n = 225$). We found significantly more corpora lutea in ovary pairs from ovulating females in the Northwest ($\bar{x} = 3.2$, SD = 0.9, $n = 38$) than in the Southwest ($\bar{x} = 2.5$, SD = 0.8, $n = 139$) Region ($t = 4.42$, df = 175, $P < 0.05$). There was a significant difference between the mean number of corpora lutea in adult females ($F = 7.181$, df = 224, $P < 0.05$) in both 1987-88 and 1991-92. Corpora luteal counts within each region did not exhibit significant year-to-year variation ($F = 1.76$, df = 138, $P = 0.13$; $F = 2.48$, df = 37, $P = 0.10$).

Mean fecundity of female martens was higher in the northwest than in the southwest (2.8 and 2.3, respectively; $Z = 2.21$, $P < 0.05$; Table 5). The statewide mean fecundity for 1989-1992 was 2.3.

Discussion

We concluded that the carcass sample voluntarily provided by Montana trappers was adequate to measure age distribution and population fecundity for

Table 3. Quantitative measures of marten reproductive tracts from Montana, 1987-93.

Age	Uterine Horn Length (mm)	95% Confidence Interval	Ovary Weight (mg)	95% Confidence Interval
0.5	29.2	28.1-30.3	9.7	8.9-10.6
1.5	40.5	39.5-41.6	14.4	13.5-15.3
2.5	46.4	45.0-47.8	16.1	15.1-17.1
3.5	49.4	46.9-51.9	18.5	16.7-20.3
4.5	51.0	48.0-54.0	15.7	13.4-18.0
5.5	44.2	40.2-48.2	16.0	13.3-18.7
6+	46.0	43.7-48.3	14.2	12.6-15.8

northwestern and southwestern Montana. Participation by trappers in the collection program was greatest in the Southwest Region where field studies on the ecology of marten were underway and regular field contacts had been established.

Wright (1963) reported that macroscopic examination of ovaries underestimates the number of corpora lutea. Our examination of a small sample of ovary pairs suggested that no significant difference existed between methods. Careful macroscopic counts of corpora lutea can provide similar results to those of microscopic examinations and did not influence the comparisons we made in this study.

The reproductive tracts of many juvenile females can be distinguished from those of adult and yearling females by the length of the cornu and weight of the ovary. Although there is some overlap, the cornu of most juveniles is smaller and diminutive as compared to that of adults. Gross morphology of the reproductive tract and the absence or presence of corpora lutea can assist in properly identifying juvenile females (Poole et al. 1994).

Ovulation rates of marten in Montana (87.1%) were similar to those reported in Ontario (87.0%) and southeast Alaska (93.0%) (Strickland and Douglas 1987, Flynn and Schumacher 1994) but higher than those reported for Quebec (79%)

Table 4. Ovulation rates by age class in martens from Montana, 1987-93.

Age Class	*n*	Proportion Ovulating
1.5	110	0.855
2.5	64	0.891
3.5	28	0.929
4+	38	0.947

Table 5. Fecundity of female marten from 1987-88 through 1991-92, for the southwest, northwest, and the entire state of Montana.

Year	Southwest Montana			Northwest Montana			Statewide		
	Proportion Ovulating	Mean CL	Mean Fecundity	Proportion Ovulating	Mean CL	Mean Fecundity	Proportion Ovulating	Mean CL	Mean Fecundity
1987-88	0.905	2.58	2.33	-	-	-	-	-	-
1988-89	0.944	2.47	2.33	-	-	-	-	-	-
1989-90	0.952	2.30	2.19	0.929	2.77	2.57	0.874	2.37	2.07
1990-91	0.923	2.75	2.54	0.923	3.17	2.93	0.909	2.90	2.64
1991-92	0.762	2.88	2.19	0.813	3.54	2.88	0.840	3.19	2.68
All Years	0.895	2.51	2.25	0.884	3.16	2.79	0.871	2.64	2.30

CL = corpora lutea

(Fortin and Cantin 1994). In our study, we found that yearling ovulation rates (85.5%) were lower than those of females ≥2 yrs (95.5%). Strickland and Douglas (1987) observed that in Ontario about 80% of yearling females and 93% of the females >1 yr ovulated. Fortin and Cantin (1994) reported that 46% of 1.5 year-old females and 92% of older females ovulated.

The average number of corpora lutea in reproductive tracts from ovulating females in Montana (2.6) was lower than that reported for the Yukon (3.3 for yearlings, 3.8 for females ≥2 yrs), Ontario (3.6), and Alaska (3.7) (Archibald and Jessup 1984, Strickland and Douglas 1987, Flynn and Schumacher 1994). The mean of 3.0 corpora lutea per ovulating female reported by Wright (1963) for northwestern Montana was similar to the mean of 3.2 for the northwest region during this study. The mean count of corpora lutea per ovulating female in southwest Montana (2.5) was well below the values reported for many other regions of North America.

Ovulation rates in Montana were similar to, or better than, those reported for other areas of North America, but mean corpora lutea counts were lower, resulting in a lower mean fecundity rate (e.g., Maine, Strickland and Douglas 1987; southeast Alaska, Flynn and Schumacher 1994; Quebec, Fortin and Cantin 1994). Furthermore, we identified significantly different fecundity rates between the Northwest and Southwest Regions of Montana. The Southwest Region exhibited more variable ovulation rates, and mean corpora lutea counts were consistently lower than those of the Northwest Region.

Montana and other Rocky Mountain states are located at the southern limit of the continental distribution of American marten (Gibilisco 1994). The southwestern region of Montana is closer to the margin of American marten distribution than the northwestern region. It may be that these fragmented habitats on the margins of marten distribution in southwestern Montana represent poorer quality marten habitat resulting in lower fecundity. We hypothesize that the distinctions in reproductive potentials between regions may be a consequence of differences in habitat quality caused by a combination of differences in prey base, habitat, and climate.

Strickland and Douglas (1987) suggested that an acceptable harvest rate is indicated by a juveniles/female ≥ 2.5 yrs ratio that is greater than the fecundity and a juvenile/female ratio ≥ 3. Fortin and Cantin (1994) evaluated the ratio of juveniles/female ≥1.5 yrs relative to trapping intensity and concurred that harvest level is acceptable when this ratio is ≥ 3. They also indicated that this age-based ratio is a better indicator of harvest intensity than sex ratios. Other studies indicated that marten are best managed by harvesting juveniles and manipulating sex ratios in the harvest to preserve females (Novak 1987). Soukkala (1983) and Archibald and Jessup (1984) noted that the sex ratio of the harvest is related to trapping pressure and when the ratio is near 1.0, or dominated by females, an

overharvest may occur. Weckwerth and Hawley (1962) indicated that the sex ratio shifted from male dominated to 1.0 during a population decline in Montana.

In northwest Montana the ratio of juveniles/female ≥2.5 yrs was below the mean fecundity, juveniles/adult female ratios were ≤ 3, and sex ratios shifted toward a female harvest during 1992-93 and 1993-94. These indices for northwestern Montana may signify population overharvests in those years. In southwest Montana, sex ratios also shifted toward parity, the ratio of juveniles/female ≥2.5 yrs did not exceed fecundity in any year, and the ratio of juveniles/female ≥ 1.5 yrs was ≤3 in all but two years. The failure to achieve a juveniles/female ≥1.5 yrs ratio ≥3 was a result of the large proportion of 1.5 year-old martens in the population. Marten harvests in southwest Montana allowed a significant percentage of juveniles to survive to the yearling age class. However, the harvest was not well-directed toward male marten. Despite skewed sex ratios in southwest Montana, our interpretation of age ratios does not support a conclusion of overharvest. These examples of 2 populations in different regions of Montana illustrate that age and sex ratio data are useful indicators of harvest but must be interpreted with care. We believe that multiple indices including age and sex, total harvest and trapping effort may provide a clearer depiction of harvest impacts in Montana.

Age distributions and sex ratios in Montana suggest that marten populations and harvests are dynamic. Changes in the proportion of juveniles in the harvest, juveniles per female ≥2.5 yrs, and juveniles per adult female indicate 2 serious population age structure shifts in southwest Montana (1989 and 1992) and one in northwest Montana (1992). Caughley (1977) indicated that a stable age distribution changes when 1 of 3 effects has occurred: survival has changed, fecundity rate has changed or changes have occurred in both. During these years, juvenile martens were not available for harvest indicating poor population productivity or survival of juvenile martens. Hawley and Newby (1957) and Weckwerth and Hawley (1962) found that declines in Montana marten populations coincided with declines in small mammal prey and decreased production and recruitment of marten. We propose 3 possible explanations for the observed age distribution shifts: prey base declines, periodic overharvest, or failure to direct harvests toward males.

Large differences in habitat quality, annual fluctuations in prey abundance and dynamic age/sex ratios among regions confound a statewide approach to the management of the American marten in Montana. Northwest Montana marten home ranges are smaller (2.9 km^2 for adult males and 0.7 km^2 for adult females; Burnett 1981) than southwest marten home ranges (35.5 km^2 for adult males and 5.8 km^2 for adult females; Fager 1991, Kujila 1993, Coffin 1994). This study found that differences in the population productivity resulted primarily from differences in fecundity of adult female martens. In addition, analysis of food habits indicates geographic variation in diet (Weckwerth and Hawley 1962, Aune and Schladweiler 1993). Management programs should reflect these significant

differences in habitat quality, population density, age and sex structure, and population productivity. Success of regional management strategies depends on accurate assessments of total harvest, sex and age structure of the harvest, trapping effort, population productivity, and diets of American marten (Strickland 1994, Fortin and Cantin 1994). Such monitoring must provide for analysis and interpretation of data by geographic region. In addition, harvest strategies must consider the degree of natural fragmentation of marten habitats and population insularity. All of these elements must be integrated into regional management programs in order to maintain a sustained-yield approach to American marten management.

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MATERNAL DEN ATTENDANCE PATTERNS OF FEMALE AMERICAN MARTENS

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Abstract: Maternal den attendance patterns of 9 radio-collared female American martens (*Martes americana*) with kits were studied in southern Wyoming from 1990-1995, using radio signals processed onto a continuous strip-chart recorder. Recorder system data showed specific dates and times of arrivals and departures of adults. Recorders operated while the kits were 1-13 weeks old. The females yielded 13 litters, 26 different den sites, and 3306 hours of den attendance data. We compared some attendance parameters between two time intervals defined as pre-weaning and weaning periods. The percent of time mothers spent at the den decreased ($P = 0.025$) from the pre-weaning to the weaning period. The average time interval ($\bar{x} \pm$ SE) spent at dens varied from 4.2 ± 0.3 to 5.7 ± 0.5 hours, whereas the average interval away from dens varied from 3.0 ± 0.2 to 4.3 ± 0.3 hours. Dens were attended for longer ($P = 0.05$) periods when kits were young. Time intervals either at the den or away from it varied from 2 minutes to 24 hours. Time of day affected den attendance patterns; females were often away from dens from dusk to midnight. Litter size had no apparent effect on the amount of time that females spent away from dens during the weeks they provided solid foods to kits. When not at dens, females were usually active but on 25 occasions we found them resting away from dens, sometimes for as long as 7 hours. Fluctuations of signal strength on strip-chart records, along with field observations, showed that females at dens engaged in nursing, playing with kits, delivering prey, and brief urination and defecation events.

Introduction

Maternal den attendance patterns are an important part of overall activity patterns for females with young. Information about animal activity is important for developing theoretical models of time-energy budgets (Jacobsen and Wiggins 1982). Energy expenditure is known to be higher for female fishers (*Martes pennanti*) with kits than for nonreproductive females, but similar information is lacking for other mustelids (Powell and Leonard 1983). An increase in female energy requirements due to developing young can add significantly to overall energy demands. Circadian activity of American marten (*Martes americana*) has been investigated (Hauptman 1979, Zielinski et al. 1983, Thompson 1986, Martin 1987) but results are inconsistent, likely due to seasonal and geographic variation. Herein we provide additional information based on 24-hour monitoring of female martens with kits.

Although den attendance could relate to reproductive success, there is scant information regarding denning behavior by female martens. Maternal inattentiveness is a primary mortality factor for fisher kits less than 1-week old in captivity (Frost 1994). Attendance patterns may be affected by environmental factors such as prey density fluctuations, snow depth, precipitation patterns, and photoperiod. Female behavior, such as adjustment of the size of core activity areas, placement of den in relation to good hunting habitat, synchronization of hunting with the peak activity of prey, and selection of den structure with good insulation properties, could also influence attendance. In addition to sleeping and eating, the kits need to learn to play, defend themselves, escape, forage, and kill prey, and acquire other developmental and social skills. Litter size and the energetic requirements of courtship and mating, which occur during this period, also could affect den attendance.

Our objective was to quantify den attendance of female martens throughout the denning period, and to determine if these patterns were related to the age of the kits, time of day, or litter size.

Methods

This research was conducted in the Medicine Bow National Forest, about 22 km south of Encampment, Wyoming. Elevations range from 2600-3300 m. Lodgepole pine (*Pinus contorta*) dominates the forest at lower elevations and Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) occur at higher elevations, or on north-facing slopes. Some of the area was logged by clearcutting and individual tree removal from 1972 to 1992. The forest is interspersed with creeks, wet meadows, dry parks, and rock outcrops. Snow depth reaches a maximum of about 2.2 m, usually in the first week of April; snow coverage persists on north-facing slopes until late June.

Radio-collared females were located at least twice per week during the denning seasons of 1990-1995. A combination of factors was used to determine natal and maternal denning (Henry and Ruggiero 1993). We placed telemetry-based activity recorders near prospective den sites to obtain presence/absence information. The recorder system consisted of receiver and digital processor (Telonics Inc., Mesa, Arizona) and a Rustrak dual-channel (pulse rate and amplitude of radio signals) strip-chart recorder (Gulton Industries, Manchester, New Hampshire). A timer circuit (Gillingham and Parker 1992) was used to designate hourly time marks on the chart tape. Power was supplied by 2 12-volt gel cell batteries, which ran the continuous records for 6 consecutive days. An omnidirectional antenna, similar to that described by Paragi (1990), consisted of 25 m of coaxial cable with the last 20 cm stripped of its outer wire shielding. The antenna would not receive radio signals more than 10 m away from den structures. The bared antenna end was placed within 3 m of the den. The weather-proof recorder box was placed 25 m from dens; therefore, the observer came no closer than 25 m to the den to check the instruments, thus reducing disturbance to the animals.

Whelping occurred throughout April. On a weekly basis, we monitored the signals for several consecutive days. We considered whelping dates as the first day we located natal dens; consequently, our estimates may be a few days later than actual whelping. Recorders were in operation from 14 April to 17 July when kits were 1-13 weeks old. When kits were >13 weeks old, females moved to new dens too frequently for the recorders to be of value. All data analyses were based on the weekly age of kits. We established 2 major age classes of kits, pre-weaning (1-6 weeks old) and weaning (>6 weeks old). During weaning females also hunted for prey to deliver to kits (Henry and Ruggiero 1993). Deployment of recorders yielded specific dates and times of the females' arrivals and departures and abandonment of dens. We were able to determine duration (in minutes) of "away" and "home" events. Any event of <5 min was ignored in the analyses. These events could be defecation, urination, or brief prey deliveries. The first and last events on each tape (chart record spool) were ignored because we did not know when that event either began or ended, respectively.

Data were disregarded from any individual not having at least 48 hours of information for either pre-weaning or weaning periods in any given year. To compare pre-weaning and weaning behavior, we used data only from females recorded during both periods in the same year. We used all data in comparing away and home events within the same period.

We compared percent time spent at dens between weaning and pre-weaning periods using 2-tailed paired *t*-tests. An arcsin transformation of the percentages prior to analysis resulted in the same *P*-value. We used Kolmogorov-Smirnov 2-sample tests to compare the duration of events in the pre-weaning and weaning periods, and the length of home and away events. *P*-values presented were

multiplied by a Bonferroni correction factor of 4. All data at a specific time of day (e.g., 0100, 0300 hours) were used to elucidate at-home patterns (Fig. 2). The number of events (n) in each cell was usually >20 (range = 6-38), and the range of proportions was 21%-85%.

Results

We obtained 3306 hours of den attendance data at 26 different sites from 9 females and 13 litters. Most martens spent a majority (>50%) of their time attending dens during both pre-weaning and weaning periods (Table 1). Percent of time spent at dens varied: 45%-75% and 38%-65% for pre-weaning and weaning periods, respectively. When considering only females observed in both periods in a particular year, we found a significant reduction ($P = 0.025$) in time spent at dens when kits were provided with solid foods.

The average duration ($\bar{x} \pm$ SE) of at home events was longer during the pre-weaning period (5.7 ± 0.5 hours, $n = 108$) than during the weaning period (4.2 ± 0.3 hours, $n = 135$). The average duration of away events was shorter during the pre-weaning period (3.0 ± 0.2 hours, $n = 112$) than during the weaning period (4.3 ± 0.3 hours, $n = 137$). Because data were not normally distributed and because short events occur more frequently than long events (Fig. 1), we also used the Kolmogorov-

Table 1. Percentage of time spent at maternal dens by female martens in south-central Wyoming.

			Pre-weaning		Weaning	
Female	Year	Kits	%	Hours	%	Hours
29	1992	2			65	(100)
37	1990	1			53	(179)
49	1991	1			51	(117)
49	1992	2	58	(82)	61	(99)
49	1993	*	66	(69)	57	(521)
49	1994	*			47	(72)
53	1993	1	45	(184)		
60	1992	2	62	(437)	38	(193)
60	1993	1			51	(244)
73	1995	1	60	(135)	38	(171)
79	1994	1	75	(229)	38	(161)
87	1994	2			44	(86)
93	1995	*	56	(227)		

*Kits died before becoming independent; litter size unknown.

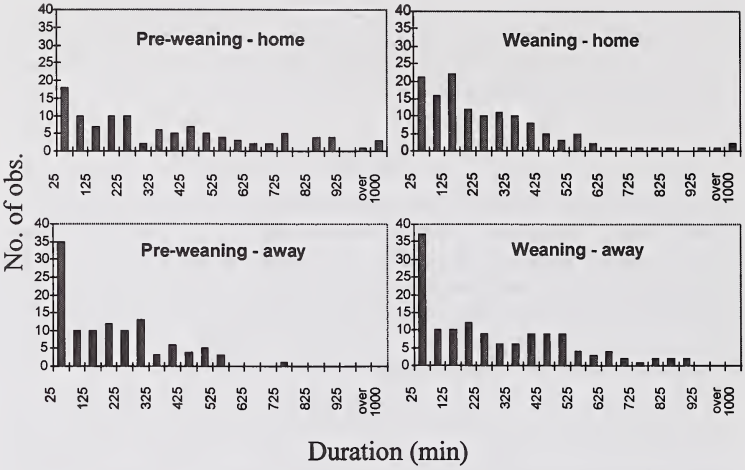

Figure 1. Frequency distributions by event length (min) of female martens in southcentral Wyoming.

Smirnov 2-sample test. Using this method, duration of home events were longer ($P = 0.04$) than away events during pre-weaning, and similar ($P = 0.62$) during the weaning period. Duration of away events did not differ ($P = 0.06$) between stages of kit development even though females were often gone for >10 hours during the weaning period. Dens were often attended for longer ($P = 0.05$) periods when kits were younger. Maximum lengths of home events were 23 hours and 18 hours, maximum length of away events were 24 hours and 15 hours for pre-weaning and weaning periods, respectively. Transitions (arrivals/departures) ranged from 1-13 times per day and were not affected ($P = 0.40$) by kit development stage.

Den attendance patterns were affected by the age of kits and the time of day (Fig. 2). As previously shown, females were more likely to be with kits when they were young. It also appears that females were usually away from dusk until midnight regardless of kit age (Fig. 2).

Due to our small sample (Table 1), no statistical tests were used to examine the effect of litter size on the amount of time spent away from dens procuring prey for kits. Time spent away was 52% and 48% for 1 kit and 2 kits, respectively, leading us to hypothesize that litter size had no influence on den attendance.

Field observations were used to supplement and interpret the strip-chart records. When not at dens, the females were usually active; however, on 25 occasions during the pre-weaning and weaning periods, we found them resting away

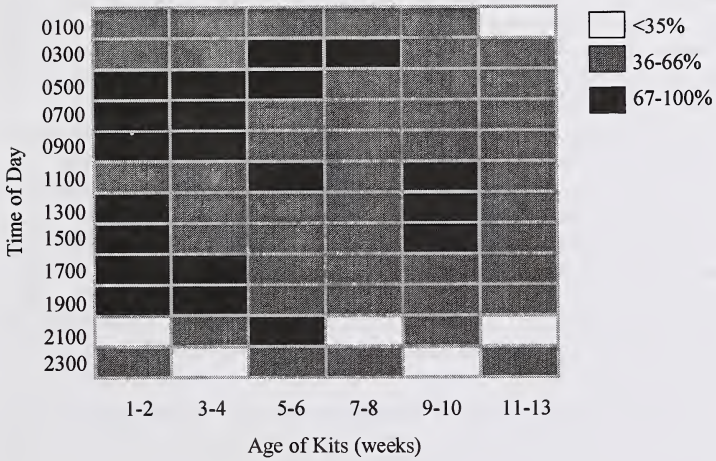

Figure 2. Den attendance patterns of female martens in south-central Wyoming, 1990-1995, as influenced by time of day and age of kits. Categories are percent "at-home" events (range: 21%-85%).

from dens, sometimes for as long as 7 hours. Fluctuations of signal amplitude (indicating activity) of ≤2 hours were on records of at home events. Females were seen and/or heard playing with older kits near den entrances. An activity period of 5-30 min frequently occurred soon after the mother's arrival and happened again before she departed.

Discussion

Our data suggest that variation in den attendance patterns is influenced primarily by stage of kit development, probably due to a dietary shift from milk to prey items. When females were nursing they often left for short periods, but, of the 22 events of >10 hours, only 1 was an away event. We observed prey deliveries on about 15 occasions (Henry and Ruggiero 1993). We suggest that prey carried to dens was intended for consumption by kits rather than the female. The longest home events during the weaning period may occur after delivery of large prey but we were unable to confirm this.

Females in dens are probably resting most of the time, assuming they are able to sleep or rest while nursing. It may be misleading to equate our away events to

activity bouts because many of the longer away events probably involved periods of resting. We have no data regarding activity of denning *versus* non-denning females. Thompson and Colgan (1994) found that 2 denning females were 35% less active than other females, based on a summer season (May to Oct.) that included pre-weaning, weaning, and non-denning periods. Compared to non-denning females, perhaps females with kits are >35% less active during pre-weaning, and possibly twice as active during the final weeks prior to kit independence. Broad categories, such as "summer," are potentially misleading particularly regarding activity patterns of females.

We could not determine an influence of litter size on den attendance patterns, but we never found a litter of more than 2 kits. We suggest that a female feeding a litter of 4 kits would be gone more often just prior to kit independence than a female with only 1 kit. Although the differences were not statistically significant, a female fisher with 3 kits was behaviorally more active than females with 1or 2 kits (Paragi et al. 1994).

Because of likely geographic variation among martens, more data would be valuable to accurately address theoretical models of energy budgets of martens attending kits. A different approach to modeling (Adair and Bissonette 1995) focused on the foraging requirements of denning martens to address factors that determine marten habitat selection. Future work relevant to this topic should compare activity patterns of denning and non-denning females.

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SURVIVAL OF AMERICAN MARTEN IN AN UNTRAPPED FOREST PRESERVE IN MAINE

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Abstract: Survival rates have been estimated for American marten (*Martes americana*) in areas with trapping and logging, but comparable data from an untrapped and unlogged area are lacking. We monitored 33 adult (≥1 yr) female and 26 adult male martens in an untrapped second-growth forest preserve (light selective cutting prior to ca. 1960, but uncut since) in north-central Maine from October 1990 to April 1994 and compared survival characteristics with an adjacent trapped population in an extensively clearcut landscape. We documented 8 mortalities during 5390 marten-days for adult females, and 4 mortalities over 10,488 marten-days for adult males within the preserve. Five of 8 adult females and 1 of 4 adult males died from predation; undetermined natural causes resulted in the remaining 6 documented deaths of adult martens. In contrast to trapped populations, annual survival rates were higher ($P = 0.01$) for males than females in the preserve. Lower survival of females was caused by higher ($P = 0.03$) annual mortality from predation relative to males. Natural mortality rates were higher in the preserve, but differences between areas were not significant ($P \geq 0.14$) for either sex. Martens do not necessarily experience lower natural mortality in areas without recent logging than in extensively logged areas. Studies that separate effects of trapping and logging are needed to assess the relative performance of populations in logged *versus* unlogged areas.

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Introduction

Understanding the dynamics of natality and mortality within unharvested populations of American marten (*Martes americana*) provides benchmarks to gauge the effects of management of exploited populations (Powell 1994). Further, knowledge of performance of marten populations in habitats of varying quality (Buskirk and Ruggiero 1994) would be enhanced with data from populations in undisturbed landscapes; such data would provide an opportunity to view selection of habitat without the confounding influences of timber harvesting and trapping. Quantitative measures of population performance, such as survival or natality, should provide the strongest comparisons between the relative quality of 2 habitats (Hobbs and Hanley 1990). But, despite much recent research devoted to marten ecology (Buskirk et al. 1994), estimates of survival rates for marten populations are limited (Hodgman et al. 1994; Thompson 1994; Potvin and Breton, this volume), and represent landscapes where habitat alteration and trapping occur simultaneously. Contemporary studies of unharvested populations in undisturbed habitats are especially important, yet, remain underrepresented in the literature (Powell 1994).

Collectively, trapping and timber harvesting may suppress marten populations where logging roads provide access to residual forests (Soukkala 1983, Hodgman et al. 1994, Thompson 1994). In these disturbed habitats, trapping may account for up to 90% of all mortalities, and may result in $\lambda < 1.0$ (Hodgman et al. 1994). In areas with high road density and intensive trapping, emigration from less intensively trapped areas may be necessary to maintain high trapping harvests (Archibald and Jessup 1984, Thompson and Colgan 1987, Hodgman et al. 1994). Trapping mortality is biased toward males (Archibald and Jessup 1984, Strickland and Douglas 1987, Thompson and Colgan 1987, Fortin and Cantin 1994, Hodgman et al. 1994), whose higher energy requirements and larger home ranges increase their exposure to trapping (Yeager 1950, Buskirk and Lindstedt 1989). Younger age classes also seem more vulnerable to trapping than older age classes (Soukkala 1983, Strickland and Douglas 1987), which over time may alter structure of harvested populations (Buskirk and Ruggiero 1994, Phillips 1994). Trapping mortality of marten also appears related to prey availability. Thompson and Colgan (1987) observed emigration among formerly resident adults that coincided with a decline in prey abundance, and as a consequence, high trapping-caused mortality among emigrants.

The effects of trapping on marten populations appears well-documented (Thompson and Colgan 1987, Fortin and Cantin 1994, Hodgman et al. 1994, Thompson 1994), yet, nonhuman (i.e., natural) sources of mortality should predominate within unharvested populations. Specific causes of natural mortality (i.e., disease, predation, starvation) and their extent among unharvested

populations need to be documented to better understand relative differences in habitat occupancy and population performance between managed and unmanaged landscapes. Further, knowledge of whether trapping mortality is compensatory or additive (Peek 1986) to natural causes is an important consideration of managers when establishing harvest regulations.

To evaluate survival characteristics for an unexploited population unaffected by recent timber harvesting, we studied a marten population within a second-growth forest preserve (light selective harvesting of large diameter eastern white pine [*Pinus strobus*] and red spruce [*Picea rubens*] at least once prior to 1960, but unharvested since) closed to trapping. Our objectives were to document causes of natural mortality, estimate semi-annual survival rates, and compare predation-caused mortality rates between sexes. We also compared survival characteristics of marten in the forest preserve with those in an intensively trapped population in an adjacent forest with extensive clearcutting (Hodgman et al. 1994).

Study Area and Methods

We studied an unexploited population of martens near the southeastern edge of their geographic range. Our study site was located in a 55-km^2 portion of Baxter State Park's forest preserve (T5 R10 WELS) in north-central Maine. Neither marten trapping nor timber harvesting had occurred in the preserve for >35 years. Terrain was undulating (330-735 m) and punctuated by low mountains. The forest was composed of coniferous (*Picea* spp., and *Abies balsamea*), deciduous (*Fagus grandifolia*, *Betula papyrifera*, and *Acer saccharum*) and mixed stands interspersed with regenerating coniferous stands that had suffered mortality from spruce budworm (*Choristoneura fumiferana*) during the late 1970's and early 1980's (Irland et al. 1988). Mature stands were 70-100 years old with some individual trees to 120 years old. Large woody debris (fallen trees) was common within 1 m of the forest floor, especially in stands regenerating from spruce budworm mortality. The forest understory varied from dense regenerating balsam fir and deciduous stems in treefall gaps to nearly open in closed canopy deciduous stands.

We also studied marten in an intensively trapped and extensively logged landscape adjacent to the western border of the forest preserve (Hodgman et al. 1994). This industrial forest was managed for softwood pulp; nearly 50% of the area had been harvested between 1974 and 1988 (Chapin 1995). The primary harvest technique was clearcutting to salvage trees damaged by spruce budworm and no protection was afforded to advanced regeneration. Furthermore, there were no limits on clearcut size prior to 1991. Selective cutting occurred in a few stands prior to our study, but the site was comprised primarily (47%) of recent (2-7 yrs old) and regenerating (8-20 yrs old) clearcuts (Chapin 1995) interspersed

with older residual stands similar in composition to stands within the preserve. Also, the industrial forest was extensively roaded (1.09 km/km^2); roads passable (i.e., spring through fall) by 2-wheel-drive vehicles bisected home ranges of 27 of 28 resident adult martens monitored during 1989-1990 (D. D. Katnik and D. J. Harrison, University of Maine, unpublished data).

In the preserve, we captured martens in 61 × 18 × 18-cm livetraps during October and November in 1990, and May, June, and late August to early October in 1991 to 1993. In the industrial forest, we live-trapped martens during May and June 1989-1990 and during September and October 1989-1991. We placed traps 20-150 m from roads and trails, and within the preserve we also trapped along transects that traversed unroaded habitat. We maintained spacing of adjacent traps at intervals of 0.30-0.65 km. Procedures for handling, fitting radio-collars, and telemetry duplicated the protocol of Hodgman et al. (1994). From all live-trapped animals, we extracted a first premolar (PM1) for age determination based on cementum annuli (Strickland et al. 1982). We also extracted an additional premolar (PM2) for cementum aging and 2 canines for radiograph aging (Dix and Strickland 1986) from all individuals retrieved after death. We monitored fates of marten in the preserve from October 1990 through April 1994. We located martens during all hours, 2-3 times weekly from May to November and, during daylight hours only at ≤10-day intervals from December to April; monitoring schedules in the industrial forest were similar (Hodgman et al. 1994). We ground-checked the status of martens that appeared sedentary for >2 locations.

We performed necropsies on all animals recovered after death. When we attributed cause of death to predation, we used a reference collection of skulls from predators known to occur on the area to match predator dentition (i.e., inter-canine width and canine diameter) with punctures on carcasses (usually the head and neck). We concluded avian predation when carcasses had puncture wounds to the torso and an absence of punctures to the skull and neck. As supporting evidence for avian predation, we considered whether the carcass had been at least partly consumed and if the carcass was recovered from the forest canopy. We attributed cause of death to an unknown predator when punctures and subcutaneous hemorrhaging could not be matched conclusively with dentition of sympatric predators and did not meet criteria for avian predation. If cause of death was not obvious, we solicited the assistance of veterinarians experienced in wildlife pathology and diseases at the University of Maine and the Southeast Cooperative Wildlife Disease Study at the University of Georgia.

We used MICROMORT (Heisey and Fuller 1985) to estimate semi-annual rates of survival and cause-specific mortality. We partitioned the year into 2 intervals: 1 May to 15 December to approximate the leaf-on season and to facilitate comparison with a marten population in an adjacent industrial forest (Hodgman et al. 1994); and 16 December to 30 April to approximate the leaf-off

season. We excluded data for the first 7 days following initial capture to minimize potential influence of handling and collaring on survival estimates (Heisey and Fuller 1985). When exact date of death was uncertain, we estimated date of death as the midpoint between date of first stationary location and date of the previous location. We excluded the fate of martens if we lost radio contact, but we included their radiodays to the midpoint between date of last location and date of first unsuccessful attempt to locate the animal. For martens that moved beyond the boundaries of the untrapped forest preserve, we used radiodays until the date the animal emigrated; thereafter, we excluded their fate. When the exact date of emigration was unknown, we used the midpoint between the last location within the preserve and the date of first location in the surrounding industrial forest.

We determined cause of mortality for all radio-collared martens within the preserve, and for all emigrants leaving the preserve. However, to enable us to compare our results with those of Hodgman et al. (1994), we restricted our survival estimates to data for adult martens during the period that they resided in the forest preserve. These individuals provided the majority of our data (93% of radiodays and 80% of deaths); further, 51 of 59 adult martens that were initially radio-collared in the preserve were never observed outside its boundaries. Because we had insufficient data to make annual comparisons, we pooled data across years. Hodgman et al. (1994) documented different rates of survival between adult male and adult female martens; therefore, we analyzed data separately for each sex.

Using *Z*-tests (Nelson and Mech 1986), we compared sex-specific daily survival rates ($\hat{s}_i$) between the 1 May to 15 December and 16 December to 30 April intervals, and annual survival rates ($\hat{s}^*$) and annual predation-caused mortality rates ($\hat{M}^*_{predation}$) between sexes. We also compared sex-specific rates of survival ($\hat{s}_{1May\text{-}15Dec}$) and natural mortality ($\hat{M}_{1May\text{-}15Dec,\ natural}$) during the leaf-on season between the population within the forest preserve and the adjacent industrial forest.

Results

We monitored 59 adult (Table 1) and 26 juvenile martens over 15,878 and 1227 marten-days, respectively. We documented 12 deaths of adults and 3 deaths of juveniles (Table 2). We attributed deaths of 2 of 5 males and 6 of 10 females to predation; 7 deaths resulted from undetermined natural causes (i.e., without proximal human influences). Within the preserve, mammals accounted for 6 of 8 deaths caused by predation; a raptor and an undetermined predator were the cause of the 2 other deaths confirmed as predation (Table 2). Among the 17 martens (8 adult females, 6 juvenile males, and 3 juvenile females) that emigrated from the forest preserve, 4 died of predation, 3 were caught by trappers, and

Table 1. Interval survival rates ($\hat{s}_i$) for adult (≥1 yr) martens during 3 time periods in an untrapped forest preserve in northern Maine, October 1990 to April 1994.

	Leaf On 1 May - 15 Dec				Leaf Off 16 Dec - 30 Apr				Annual 1 May - 30 Apr			
Sex	*n*	Marten-days	$\hat{s}_i$	95% CI	*n*	Marten-days	$\hat{s}_i$	95% CI	*n*	Marten-days	$\hat{s}_i$	95% CI
Male	26	6914	0.94	0.85-1.00	23	3574	0.93	0.83-1.00	26	10,488	0.87	0.75-1.00
Female	33	3870	0.84	0.68-1.00	17	1520	0.64	0.43-0.95	33	5390	0.53	0.34-0.83

Table 2. Cause of death for martens within an untrapped forest preserve in northern Maine, October 1990 to April 1994.[a]

Source	Adult[b] Females	Adult Males	Juvenile[c] Females	Juvenile Males	All Martens
Predation					
Canis latrans	0	1	1[d]	0	2
Martes pennanti	1	0	0	1	2
M. americana	2	0	0	0	2
Raptor	1	0	0	0	1
Unidentified	1	0	0	0	1
Unk. Natural Cause	3	3	1	0	7
Total	8	4	2	1	15

[a] Excludes deaths of emigrants.
[b] ≥1 year.
[c] <1 year.
[d] Confirmed canid: most likely *Canis latrans* although possibly *Vulpes vulpes*.

1 died of unknown natural causes; we could not determine the fates of 9 martens that emigrated from the preserve because of loss of radio contact.

Within the forest preserve, $\hat{s}_i$ was not different between the leaf-on and leaf-off seasons for either adult males ($\hat{s}_{1May\text{-}15Dec} = 0.999$, $\hat{s}_{16Dec\text{-}30Apr} = 0.999$, $Z = 0.61$, $P = 0.54$) or adult females ($\hat{s}_{1May\text{-}15Dec} = 0.999$, $\hat{s}_{16Dec\text{-}30Apr} = 0.997$, $Z = 1.64$, $P = 0.10$). Therefore, we pooled survival rates for the 1 May to 30 April interval within each sex for subsequent comparisons within the forest preserve.

In contrast to an adjacent population that was intensively trapped (Hodgman et al. 1994), adult males in the preserve exhibited higher ($P = 0.01$) annual survival rates ($\hat{s}^* = 0.87$, 95% CI 0.75-1.00) than adult females ($\hat{s}^* = 0.53$, 95% CI 0.34-0.83). Lower survival rates for adult females than for adult males within the forest preserve resulted from higher ($P = 0.03$) predation-caused mortality rates of adult females ($\hat{M}^*_{predation} = 0.29$, 95% CI = 0.08-0.50) relative to adult males ($\hat{M}^*_{predation} = 0.03$, 95% CI = 0.00-0.10).

In the 1 May to 15 December interval, survival rates (Table 1) were higher for both adult males ($Z = 9.64$, $P < 0.001$) and adult females ($Z = 3.32$, $P = 0.001$) within the untrapped population in the preserve compared to the adjacent industrial forest. Further, natural mortality rates within the preserve (adult male $\hat{M}_{1May\text{-}15Dec,\,natural} = 0.06$, 95% CI 0.00-0.15; adult female $\hat{M}_{1May\text{-}15Dec,\,natural} = 0.16$, 95% CI 0.00-0.32) exceeded rates within the industrial forest (adult male $\hat{M}_{1May\text{-}15Dec,}$

$_{natural}$ = 0.00; adult female $\hat{M}_{1May\text{-}15Dec,\ natural}$ = 0.07, 95% CI 0.00-0.20); however, differences were not significant (P = 0.14, adult males; P = 0.39, adult females) and power was low.

Discussion and Implications

Although we observed no significant differences between survival rates during the leaf-on and leaf-off seasons within the preserve, survival rates were lower during the leaf-off season for both sexes. Low power resulting from few deaths in the preserve likely contributed to the lack of significance. We consider winter to be the most limiting season for marten in northern Maine, and the trend in daily survival rates for females supports this suggestion.

Researchers have noted that both American marten (Hargis and McCullough 1984, Katnik 1992, Thompson and Harestad 1994) and Eurasian pine marten (*Martes martes*) (Pulliainen 1981, Brainerd et al. 1994) avoid meadows and recently harvested forests that lack overhead cover and structural diversity near the ground. Hargis and McCullough (1984) and Pulliainen (1981) suggested that avoidance of forest openings lowers predation risks from raptors. However, few incidences of avian predation have been documented (Thompson 1994; F. Potvin, pers. commun.), and for Eurasian pine marten, these were generally restricted to less abundant larger birds of prey (Korpimaki and Norrdahl 1989). Populations of weasels (*Mustela* spp.) may be influenced by raptor predation (Powell 1973); however, no one has presented empirical evidence that avian predators inflict significant mortality on medium-sized mustelids such as marten. In our study, mammalian predators, including other martens, were the principal sources of mortality. For unexploited populations in forest communities similar to ours, habitat selection by marten may be associated with reduced exposure to mammalian rather than avian predators. Martens within the preserve exhibited selection for spruce-budworm damaged stands characterized by extensive vertical and horizontal structure, but with overstory canopy closure of 10-50% (Chapin 1995). Thus, forests with horizontal and vertical structure that provide escape cover, but do not necessarily have an intact overstory, may be more important to marten than previously considered. But, even with this degree of forest structure, adult females in the preserve suffered high natural mortality.

In Maine, terrestrial furbearers are harvested during an 8-week season beginning approximately 1 November. Trappers frequently pursue fisher (*M. pennanti*) and marten simultaneously (Krohn et al. 1995), and although fisher occur at lower density in our study area than in other parts of Maine (Krohn et al. 1995), predation by fishers (i.e., on residents plus emigrants, n = 3) and other martens (i.e., on residents, n = 2) resulted in nearly half of the documented incidences of

predation (i.e., on residents plus emigrants, $n = 12$) of our radio-collared martens. Among exploited populations, trapping may lower densities of conspecifics and of some potential predators of marten; this effect may lower the subsequent mortality of martens that survive the trapping season. Thus, we speculate that trapping may have community-level effects that may partially compensate for the higher human-caused mortality in some harvested populations.

We observed substantial emigration (8 of 33) of adult females from the forest preserve (5 during December to March and 3 during July to September). At least 2 females abandoned established ranges following independence of their offspring; however, no resident adult males left the preserve (Phillips 1994). Thompson and Colgan (1987) observed emigration of both sexes of resident marten during a period of prey scarcity. Furthermore, we observed substantial mortality of transient females (3 of 8) and speculate that transients experience lower survival than would be expected for residents. Similarly, Potvin and Breton (this volume) observed lower survival rates for dispersing than resident male martens in western Quebec. Our sex-biased emigration pattern likely increased natural mortality of transient females relative to males, which all maintained resident status. Even among residents within the preserve, females experienced higher rates of natural mortality (Table 1); 8 of 12 adult martens that died of natural causes were females (Table 2). Thus, dynamics within untrapped areas appear to be complex, and should be considered before reservoirs are adopted as a primary conservation strategy for marten.

Much discussion of the reservoir strategy for management of marten populations (Archibald and Jessup 1984, Thompson and Colgan 1987, Buskirk 1993) has occurred since it was first presented by de Vos (1951). Buskirk (1993) has cautioned that, because the strategy can be employed without detailed population monitoring (i.e., simply set aside areas which are closed to trapping), managers may falsely conclude that populations within reservoirs are stationary. However, viability of metapopulations may suffer if emigrants never reach other reservoirs because mortality in areas between reservoirs is high (Buskirk 1993, Lyon et al. 1994). Although dispersing animals could help to maintain high harvests in areas adjacent to reserves (Archibald and Jessup 1984, Thompson and Colgan 1987, Hodgman et al. 1994), we documented that nearly half (8 of 17) the martens leaving the forest preserve died, primarily from trapping and intra- and interspecific aggression. Further, transient individuals (i.e., those without an established home range) may forage less efficiently because of a lack of familiarity with foraging areas. Hence, effect of reservoir size, environmental and genetic variability, and habitat quality are important considerations that will influence source-sink dynamics (Pulliam 1988) and ultimately any management strategy for marten that is based on reservoirs. We suggest that in landscapes with high road densities and intense trapping pressure, additional conservation measures, such as

quota systems (if enforceable), may be needed to supplement a reservoir strategy for marten management in the context of source-sink dynamics.

Thompson (1994) found lower natural and trapping mortality in unlogged than logged forests. Similarly, Potvin and Breton (this volume) reported that male martens had lower rates of natural mortality in unlogged forests than in logged forests. However, unlogged sites in both studies were open to trapping; thus, the vulnerability of marten to trapping complicates any assessment of natural mortality. Further, effects of trapping appear confounded with forest harvesting because trappers use logging roads to access residual marten habitat (Hodgman et al. 1994, Thompson 1994). We also observed higher survival of marten in our "unlogged" forest; however, the differences were attributable to higher trapping mortality in the logged forest. Furthermore, estimates of natural mortality were higher for both males and females in the forest preserve, but power was low and differences were not statistically significant. Thompson (1994) concluded that marten prefer old conifer forests because marten are better able to avoid predators in less open unlogged stands. Our data do not support this conclusion and we stress the need for study designs that separate the effects of trapping and timber harvesting on survival and productivity of marten populations.

The uncut forests in Thompson's (1994) study were 150-250 years old and of fire origin, whereas our forest preserve site was mature, but the most merchantable large volume eastern white pine and red spruce had been selectively removed several decades prior to our study. Older forests in Ontario may be structurally different than the second-growth forests of northern Maine, and these differences could impart a unique survival advantage to Ontario marten. However, viable marten populations occur throughout much of northern Maine, despite the relatively young forests of that region. The presence of regenerating spruce budworm-affected stands may offer structural complexity to these younger second-growth stands and provide roughly similar habitat conditions as older boreal forests of Ontario. Forest structure required by marten may not be limiting in Maine's second-growth forests (Chapin et al., this volume); therefore, relationships between forest age and marten survival are probably region specific.

We recognize the limitations of our comparisons of natural mortality between the 2 sites given the intense trapping pressure in the industrial forest. Human-caused mortality in the industrial forest may have been so high (45 of 49 deaths) that it may have compensated for the few natural mortalities (only 4 of 49 deaths were attributed to natural causes), and thus masked any effects of habitat on survival. Densities of fishers also may have been affected by lower habitat quality on our study site relative to other regions of Maine (Krohn et al. 1995) and by intensive trapping in the industrial forest site. Fewer fishers may have lowered natural mortality rates of the marten. These findings also highlight the importance of understanding the influence of trapping and its effects on marten populations.

Katnik (1992) and Chapin (1995) reported that marten on our industrial forest site exhibited strong landscape-scale selection for large blocks of intact forest. Hence, we conclude that marten in harvested landscapes may survive as well as marten in habitats without logging, provided that associated human access does not result in trapping harvests that exceed sustainable levels. Trapping mortality (Hodgman et al. 1994) coupled with landscape-scale habitat selection resulted in substantially lower marten densities in our industrial forest site (Phillips 1994) where trapping and timber harvesting occurred simultaneously; however, home range size and proportion of adult females that were lactating did not differ between sites (Phillips 1994). Our data suggest that individual martens may be able to survive as well in residual forests within extensively logged landscapes as in forest preserves. However, controlled studies are needed to isolate the effects of trapping and timber harvesting so that the 2 activities can be managed simultaneously to ensure future viability of marten populations in both managed and unmanaged forests.

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FACTORS AFFECTING THE REPRODUCTIVE SUCCESS OF CAPTIVE FEMALE FISHERS

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Abstract: We assessed the reproductive success of 14 adult (≥2 years old) female fishers (*Martes pennanti*) captured from the wild and brought into captivity, 1990-1993. All fishers were kept at the same nutritional level and fed a standardized diet of commercial mink (*Mustela vison*) feed, beef liver, and venison (*Odocoileus virginianus*). All females were parturient at the time of capture and gave birth in the spring after initial capture. Females were significantly heavier after giving birth than at time of capture ($P = 0.006$). Mean litter size was 2.7 (SE = 0.22; range = 1-4). The sex ratio at birth ($n = 38$) did not differ from 50:50 ($P = 0.33$) and body weight between sexes was not different at birth ($P = 0.64$). Nine of 15 kit mortalities occurred within the first week of life. Causes of mortality were exposure, lack of parental care, and cannibalism by the mother. Maternal age was weakly correlated with litter size ($r^2 = 0.29$, $P = 0.06$) and the number of kits surviving to 1 day of age ($r^2 = 0.39$, $P = 0.03$). The ratio of litter weight to maternal weight had a positive correlation with litter size ($r^2 = 0.78$, $P < 0.001$). Although the nutritional status of the reproductive female likely plays a major role, other factors including litter size, litter weight, and maternal age also influence the reproductive success of adult female fishers.

Introduction

Reproductive success is the combination of biological and environmental factors that can increase or inhibit the reproductive capability of an individual. Clutton-Brock (1988) outlined phenotypic factors that are commonly related to reproductive success in both males and females: age, body size, dominance rank, mate choice, and early development. In addition, there are many other environmental, nutritional, and behavioral factors that can also affect an individual's reproductive success (Kirkpatrick 1988). The combination of all these factors

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can determine how successful an individual is in producing offspring. Many of these components vary among years and throughout an individual's life time.

Fishers (*Martes pennanti*) present a variety of problems when trying to evaluate reproductive success because of their body size and shape, social behavior, intra-sexual distribution, mating patterns, and reproductive strategies. Because of their long, thin bodies, fishers have a high surface to volume ratio, high convective heat loss, and high energy requirements (Powell 1993). Fishers exhibit intrasexual territoriality throughout most of the year except during the breeding seasons when male territories greatly increase in size (Arthur et al. 1989). Reproductive patterns of female fishers are characterized by delayed reproduction (earliest litter at 2 years of age), long period of embryonic diapause (10-11 months), short active development period (34-42 days), and small litters (range = 1-4, $\bar{x}$ = 2.7) (Douglas and Strickland 1987, Powell 1993, Frost 1994). Although fishers are physiologically capable of breeding and raising young each year, whether they do so is a function of the factors outlined above.

The purpose of this study was to control for environmental and nutritional effects and then test for differences in the remaining phenotypic effects. Specific factors identified were maternal age and weight, litter size and weight, and the interactions between maternal age and weight with litter size and kit survival. We classified a female as being successful during a reproductive period if at least 1 of her kits survived to 1 year of age (earliest age of sexual maturity).

Methods

Thirty-seven female fishers were purchased during the fall trapping seasons of 1990-1992 from trappers in central and eastern Maine (Frost and Krohn 1994). All animals were housed at the University of Maine's Animal Research Facility in Orono, Maine. Fishers were housed individually in pens located under conifer tree cover and were exposed to external temperatures and natural photoperiod. Each cage was 1.2 m wide by 1.2 m tall by 2.4 m long, wrapped with 14-gauge, 2.54-cm^2 wire mesh, and was elevated approximately 10-20 cm above the ground. Maternal nest boxes were equipped with plexiglass windows so that observations of kits could be made with minimal disturbance to the animals. Daily rations were comprised of a prepared chow consisting of 50% commercial mink (*Mustela vison*) feed, 40% venison (*Odocoileus virginianus*), and 10% beef liver fed at approximately 100 g/day. Water was given *ad libitum* and changed daily. See Frost and Krohn (1994) for additional details on care and handling of captive fishers. This research was done in accordance with an approved animal welfare protocol at the University of Maine.

Ages of fishers were initially estimated from examination of the sagittal crest and later from cementum annuli using the first premolar (Arthur et al. 1992).

Adults (≥2 years old) were weighed immediately after capture and at least once a month thereafter or whenever the kits were weighed. In February of each year, pregnancy tests (ICG Canine Genetics, Inc., Malvern, Pennsylvania; use of manufacturer's name does not imply US Government endorsement of commercial products) and ultrasound readings (Frost 1994) were done on all fishers determined to be ≥1 year old. Maternal nest boxes were monitored daily beginning the first week of March of each year until all pregnant females had given birth. In 1991, kits were not examined until they were about 2.5 weeks old. In 1992 and 1993, kits were examined 24-48 hours postpartum. All kits were raised by their mothers. Fishers were attended to daily and when mortalities occurred, the animals were removed and taken immediately for necropsy to the Cooperative Extension Pathology Laboratory, University of Maine, Orono.

All measurements are expressed as means ± SE. We pooled data among years because sample sizes were small. Chi-square analysis was used to test differences between sex ratios at birth. A Mann-Whitney *U* test was used to compare maternal weights at the time of capture and at birth and to compare body weights of male and female kits at birth. A Kruskal-Wallis test was used to evaluate the number of kits alive among preselected periods. Pearson's correlation was used to compare maternal age and body weight with litter size and litter weight. Statistics were calculated using SYSTAT statistical software (Wilkinson 1990).

Results

Ages of fishers at capture ranged from 6 months to 3.5 years and 14 of the 37 females were estimated to be ≥1.5 years old. Mean maternal body weight was greater after giving birth (2565.8 ± 90.04 g) than at time of capture (2206.5 ± 57.04 g, $U = 86.5$, $P = 0.006$). All 14 adults were pregnant, as evidenced by increased progesterone levels and positive ultrasound observations (Frost 1994) and subsequently gave birth. Five litters with a total of 11 kits were born in 1991; 7 litters produced 23 kits in 1992; and 2 litters produced 4 kits in 1993. Birth dates ranged from March 4 to April 1 for all 3 years with a mean birth date of March 24 (± 2 days) (Table 1). Litter size ranged from 1 to 4 kits with a mean litter size of 2.7 ± 0.22. Twenty-two males and 16 females were born; however, the sex ratio was not significantly different from 1:1 ($\chi^2 = 0.95$, $P = 0.33$) (Table 1). All kits in 5 of the 14 litters were the same sex (Table 1). There was a weak positive correlation between maternal age and litter size ($r^2 = 0.29$, $P = 0.062$).

Fifteen of the 38 kits died before reaching an age of 1 year (Table 1). Of those, 9 died within 7 days of birth. Seven appeared to die of exposure and 2 were cannibalized by their mother (Table 1). Of the remaining mortalities, 1 was found abandoned out in the cage at 24 days of age, 2 were cannibalized by their mother at 68 days of age, and 2 died shortly before they were 1 year old (Table 1).

Table 1. Birth dates, sex ratios, and number and causes of mortalities of captive-born fisher kits through their first year, 1991-1993.

Year[a]-ID# (Age[b])	Birth Date	Sex		Litter Size	Number Alive				Cause of Death (number of kits)
		Male	Female		Birth	7 Days	30 Days	1 Year	
91-713 (2)	4 March	2	1	3	3	0	0	0	exposure (3)
92-737 (2)	18 March	0	2	2	2	2	2	1	anaphylactic shock (1)
92-732 (3)	21 March	2	0	2	2	2	2	2	
91-712 (2)	22 March	2	1	3	3	1	0	0	cannibalized (2) abandoned (1)
91-715 (3)	23 March	0	2	2	2	2	2	2	
93-769 (2)	24 March	1	0	1	0	0	0	0	stillborn (1)
92-733 (2)	25 March	1	2	3	3	3	3	3	
91-716 (2)	26 March	1	1	2	2	2	2	2	
92-734 (3)	26 March	0	3	3	3	3	3	3	
92-736 (3)	27 March	3	1	4	4	4	4	2	cannibalized (2)
91-711 (3)	28 March	3	0	3	3	3	3	2	malabsorption (1)
92-742 (4)	28 March	3	1	4	4	2	2	2	exposure (2)
92-735 (2)	31 March	2	1	3	3	1	1	1	exposure (2)
93-765 (3)	1 April	2	1	3	3	3	3	3	
Total		22	16	38	37	28	27	23	
Mean	24 March			2.7	2.6	2.0	1.9	1.6	
SE	2 days			0.22	0.27	0.31	0.34	0.29	

[a] Year female was captured.

[b] Maternal age at time of birth.

Maternal age had a weak positive correlation with the number of kits surviving to 1 day of age ($r^2 = 0.39$, $P = 0.033$).

Mean body weight of kits ≤48 hours old in litters that included at least 1 live kit ($n = 9$) ranged from 36.5 ± 0.50, to 58.0 ± 0.58 g (Table 2). Body weights of kits measured within 48 hours of birth were not different ($U = 117.5$, $P = 0.64$) between males and females. Litter weight ranged from 73 to 209 g with a mean of 145 ± 16 g (Table 2). The ratio of litter weight to maternal weight had a positive correlation with litter size ($r^2 = 0.78$, $P < 0.001$).

Discussion

Reported parturition dates for fishers range from mid-February to May (Powell 1993). Fur farm records from British Columbia show most births occurred in March and April (Hodgson 1937, Douglas 1943). Paragi et al. (1996) reported the birth of 12 litters in the wild between March 3 and April 1 in south-central Maine. All litters during this study were also born between March 3 and

Table 2. Relationships between maternal weight and litter characteristics for 9 litters of fishers, 1991-1993.

Year	Female I.D.	Litter Size	Maternal Body Weight (g)[a]	Mean Kit Body Weight[a] ± SE (g)	Litter Weight (g)	Litter Weight/ Maternal Weight (× 100)
1991[b]	F713	3	2370	46.33 ± 3.18	139	5.86
1992	F732	2	2563	40.00 ± 0.00	80	3.12
	F733	3	2200	55.00 ± 2.65	165	7.50
	F734	3	2500	58.00 ± 0.58	174	6.96
	F735	3	3000	41.00 ± 3.79	123	4.10
	F736	4	2900	52.25 ± 1.38	209	7.21
	F737	2	2279	36.50 ± 0.50	73	3.20
	F742	4	2912	51.50 ± 1.50	206	7.07
1993[c]	F765	3	2592	46.67 ± 3.37	140	5.41
Mean		3	2591	47.47	145	5.60
SE		0.24	97	2.43	16	0.58

[a] Weight measured 1-2 days after giving birth.

[b] Four litters were not weighed until 2 weeks after birth.

[c] One litter with 1 stillborn kit not included.

April 1. Mean birth dates did not differ between wild fishers (Paragi et al. 1996) and captive fishers ($U = 49.5$, $P = 0.075$) in Maine. Because photoperiod may synchronize implantation within a population (Mead 1989) and day length varies with latitude, implantation and parturition may also vary with latitude (Powell 1993).

Estimates of mean litter size are a function of the index used to evaluate them. Mean litter sizes across the fisher's range are between 2.0 and 3.0 (Powell 1993). We found mean litter size at birth was 2.7 (range of 1-4) but by 7 days postpartum it had decreased to 2.0. In general, field studies done to date may not have detected actual litter size at birth. Fur farms, again, provide the most reliable data on litter sizes since date of birth is generally better known than in field studies. Hall (1942) reported litter sizes in captive fishers ranging from 1 to 4 ($\bar{x} = 2.7$). Wright and Coulter (1967) reported 1 fisher with 5 corpora lutea and Hodgson (1937) reported a litter of 6. Embryos may start to develop, but may then be resorbed (Frost 1994); thus, litter sizes derived from placental scars and litter sizes at birth may differ. Litter size at birth does not necessarily indicate reproductive success. If kits do not survive to be recruited into the population and to reach sexual maturity, then reproduction of the adults has not been successful.

Sex ratios for fishers are usually determined from harvested populations (Douglas and Strickland 1987) in association with fur harvests. Krohn et al. (1994) reported that juvenile fishers are more vulnerable to trapping than adults which results in age ratios of harvested animals being biased toward juveniles; however, they also reported that trapping vulnerability of juveniles was not different between sexes. This result suggests that sex ratios of harvested juveniles should reflect the population sex ratio. In Maine, sex ratios of harvested juveniles are 50:50 (Maine Department of Fish and Wildlife, unpublished data). Strickland et al. (1982) also reported an equal sex ratio of 163 kits born in captivity, which is consistent with this study.

Rates and causes of mortalities in newborn fishers are not well documented. The mortalities we documented in the first week of life were caused by improper care by the mother, cannibalism by the mother, or cold and wet weather. The earliest kits born, all of which died, were born on March 3, when a severe ice storm occurred. Whether the mortalities were caused by inattentiveness of the mother, harsh weather conditions, or improper nesting material could not be determined. We presumed the nest box condition was as good or better than most dens in the wild. The other mortalities from freezing were apparently from improper care by the mother. The kits were buried in nesting material away from the other kits and although 2 were revived, they died the next day. Two kits were also cannibalized immediately after birth. They were observed the day they were born but were not handled so we do not know if they were dead; however, the next time the nest box was observed there was only 1 kit instead of 3.

Not all adult female fishers successfully raise young in the wild each year (Paragi 1990, Arthur and Krohn 1991). The percentage of females estimated to give birth annually in the wild varies based on what reproductive index is evaluated (Douglas and Strickland 1987, Crowley et al. 1990, Paragi 1990, Powell 1993, Frost 1994). All adult females in the current study that were brought into captivity and were old enough to have been bred the previous year (>1 year old) gave birth. This success was probably due to the constant availability of high-quality food fed to them in captivity. Fishers need to hunt throughout the winter and the severity of the winter may affect how many females give birth in the spring (Krohn et al. 1995). In reviewing the literature, Kirkpatrick (1988) found that in other carnivores poor nutrition resulted in the delay of puberty, differential breeding rates, smaller litter sizes, and higher offspring mortality. Elowe and Dodge (1989) found that abundance of fall mast crops affected the reproductive output the following winter in black bears (*Ursus americanus*). Although few data are available on the nutritional effects of reproduction for fishers, we assume they would react similarly to other carnivores. Powell and Leonard (1983) developed a model of energy expenditure for reproduction in fishers; however, it was tested on only 1 reproducing female. They reported that energy expenditures for a reproductive female ranged between 2.3 and 3 times that of a nonreproductive female, and concluded that these energy requirements were related to body size constraints. Because of their long and slender body, fishers have a high energy requirement during reproduction. Poor nutrition may affect them more than other carnivores.

Kits were not handled in previous studies dealing with captive fishers until 1-4 weeks after birth; thus few data are available on kit or litter weight at birth. We handled kits within 48 hours of birth (Frost 1994). The ratio of litter weight to maternal weight is a measure of maternal investment. Smaller species should have a higher ratio of litter weight to maternal weight and larger species should have a lower ratio. As predicted, martens (*Martes americana*) exhibit a higher ratio (9.5) and wolverines (*Gulo gulo*) show a lower ratio (2.7) (Oftedal and Gittleman 1989). Gittleman (1986) reported the ratio of litter weight to maternal weight for fishers as 3.4, whereas we found that it was 5.6. Oftedal and Gittleman (1989) obtained data from different litters and different populations, over a wide geographic area and different habitats, which could bias the results. Our data were collected from litters in a small geographic area in a homogenous habitat.

Our measure of parturition rate (100%) was probably biased upwards because of the captive feeding regime employed. Arthur and Krohn (1991) found that the maximum parturition rate for wild fishers ≥2 years of age in Maine was 75% and York (1996) reported a mean parturition rate of 68% in Massachusetts. They hypothesized that when fishers are under stress from cold temperatures or limited food availability, pregnancy may be interrupted (Arthur and Krohn 1991). Rogers (1976) suggested a physiological threshold that determines whether

pregnancy will be terminated in black bears. Fishers exhibit delayed implantation, which results in little maternal energy being invested in reproduction until after implantation. Physiologically, fishers may be able to determine whether they can invest a large amount of energy into reproduction. If they can, the ratio between maternal weight and litter weight should vary under different nutritional and energy levels. Delayed implantation may be a mechanism that allows females to maximize their fitness by producing large litters in good years, smaller litters in poor years, and not reproducing at all in extremely poor years.

There is evidence to support the hypothesis that female body size in mustelids is limited by energy requirements and expenditures, especially during reproduction (Erlinge 1979, Moors 1980, Powell and Leonard 1983). If body size is limited energetically in fishers and larger litters are produced by larger females, then litter size should also be limited in fishers. In wild fishers, maximum litter size appears to be 4 (Douglas and Strickland 1987, Powell 1993). In other carnivores (Lunn and Boyd 1993, Derocher and Stirling 1994), maternal weight and body size increase to a certain age and then decrease. In fishers, females reach their adult weight by the end of their first year (Frost 1994). Therefore, age should have little effect on maternal weight unless older females have larger litters. We found a positive correlation between maternal age and litter size. This result could be due to older females having established territories, with known food sources, and better hunting abilities that would enable them to maintain a higher, more energetically expensive weight resulting in larger and heavier litters and ultimately increasing their reproductive success.

Acknowledgments

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SOCIAL ECOLOGY OF THE STONE MARTEN IN CENTRAL ITALY

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Abstract: The social ecology of the stone marten (*Martes foina*) is discussed based on research carried out in central Italy. The study was conducted by means of radio telemetry, scat analysis, and habitat use analysis; internal anatomy of home ranges was analysed by the kernel estimator. The stone marten showed intrasexual territoriality. Two aspects of the observed spacing patterns were unexpected: the coincidence of space use within the mating pair, which contradicts a hypothesis of spatial segregation between sexes, and the limited seasonal variations of males' territories, which contradicts a hypothesis of a roaming strategy. Furthermore, we recorded frequent association of the male with cubs in the den, association of the male with young during their first months of life, and an increased activity of the male when the female reduced her activity during lactation. We postulate a male parental investment that could account for the recorded spacing patterns. A male parental role can strongly affect the social pattern of the species, although such cooperation is unlikely to be essential for successful rearing of young, as suggested by the variation in the number of females per male.

Introduction

The stone marten (*Martes foina*) displays intrasexual territoriality (*sensu* Powell 1979, Skirnisson 1986, Krüger 1990, Herrmann 1994) similar to that of most *Martes* populations so far investigated (Balharry 1993, Powell 1994). Territoriality can occur if a limiting resource exists and if the cost of territorial defence is balanced by the benefit accrued from monopolizing a resource through the exclusion of conspecifics. Therefore, intraspecific competition appears to be a key factor in the evolution of territoriality, particularly in the case of predators that exploit resources (prey) which are generally scarce and dispersed, and often

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react to predation with depression (*sensu* Powell 1994). Intrasexual territoriality is characterized by the overlap of the male and female home ranges, which does not exclude competition for resources in the overlapping territories. An economic benefit is therefore expected to balance the cost of intraspecific competition. In particular, the following benefits can be suggested: (1) familiarity within the mating pair, which increases the probability of reproduction (Powell 1994); (2) common defence of territories; and (3) increased survival of young because of male parental investment. Furthermore, some mechanisms could reduce intersexual competition, thus allowing for the evolution of intrasexual territoriality in the presence of minor benefits: (1) differences in the trophic niches of sexes, although data so far available for *Martes* reject this hypothesis (Powell 1994); and (2) spatial segregation between sexes as observed for stoats (*Mustela erminea*) (Erlinge 1977), black bears (*Ursus americanus*) (Rogers 1987), and grizzly bears (*Ursus arctos horribilis*) (Wielgus and Bunnell 1995). Unfortunately, few published data quantify the intensity of home range use in *Martes* spp. (Balharry 1993). The different adaptive roles for the two sexes represent another factor strongly affecting the carnivores' territoriality patterns. Sandell (1989) proposed that, whereas females disperse in respect to trophic resources and tend to defend a territory large enough to support them and their young, males tend to defend the largest possible territories to include (and control) the greatest number of females, which are a key resource. This model appears to be confirmed by the roaming strategy of males, as recorded for several felids and for the stoat (see Sandell 1989), which is characterized by a remarkable enlargement of the home range during the mating season, and is thought to increase the possibility of mating with more females.

The objective of this study was to review the social organization of the stone marten by determining: (1) the spatial segregation within the mating pair, and (2) the seasonal variation in the home ranges of males.

Materials and Methods

From October 1990 to February 1995 we studied the ecology of the stone marten in a forested and rural area of central Italy. Twenty animals were trapped in box traps (23 × 23 × 125 cm), and 16 individuals (11 males, 5 females) were fitted with radio-collars (MOD 080 and MOD 070; Telonics, Mesa, Arizona) and intensively radio-tracked. We collected 5782 single locations (fixes). Moreover, 134 continuous all-night observations were conducted, during which the animals were located every 15 min, resulting in 8050 fixes. The independence interval between successive fixes (Swihart and Slade 1985) was estimated as the average time interval (6 h 48 min) needed to travel the maximum distance within the home range (minimum convex polygon: MCP), moving at average speed, as

calculated from continuous locating sessions (White and Garrott 1990). To assess the internal use of the home range, we selected a subsample of independent fixes, excluding day-resting sites, and analysed them using the kernel estimator (Worton 1989), as calculated using the software GRID (Swiss Ornithological Society 1994; parameters: grid = 50 × 50 m, SD = 125 m). To measure the coincidence of space use among individuals, we considered the kernel estimator as an estimate of space use probability and calculated the spatial niche overlap using Horn's index of overlap (Horn 1966), which is based on information theory. For each pair of individuals we established a grid that included both home ranges; we calculated, for each point on the grid, the kernel estimator (proportion of space use) for both individuals. We considered the two values of kernel obtained for each point (i) of the grid as the proportions (p_{ij}, p_{ik}) of the resource i in the total resources used by individuals j and k, and the Horn's index was calculated. Thus, for each pair of individuals an index ranging from 0 (no coincidence in space use between the two individuals) to 1 (complete coincidence) was obtained. The relationship between spatial-niche overlap and home-range overlap (100% minimum convex polygon) was investigated using regression analysis (Sokal and Rohlf 1995). The Wilcoxon 2-sample test (Siegel and Castellan 1988) was used to assess between-sex differences. Seasonal variations in home range were analyzed by dividing the year into 6 2-month periods (thus obtaining similar samples of fixes per period), based on the reproductive biology of the species (Mead 1994): gestation (15 February to 15 April), lactation (15 April to 15 June), rutting (15 June to 15 August), and diapause 1, 2 and 3 (15 August to 15 October, 15 October to 15 December, and 15 December to 15 February, respectively). To avoid assumptions about distribution, seasonal differences were tested using a non-parametric ANOVA (Kruskal-Wallis), whereas between-sex differences were tested with a Wilcoxon 2-sample test.

Results

All adults of the same sex used exclusive areas. Adult males' home ranges overlapped with those of 1 or 2 females (Fig. 1); because in these cases we recorded association between the 2 sexes and reproduction of females, we define an adult male and an adult female with overlapping home ranges and that reproduced in the study period as a mating pair. Because the home range of a male may overlap more than 1 female home range, allowing the male to be part of more than 1 mating pair, we define a male/female nucleus as a male and 1 or more females with which it has persistently overlapping home ranges. We identified several male/female nuclei by simultaneously tracking animals with overlapping ranges (Fig. 1). M7 and F5 were tracked simultaneously for 338 days.

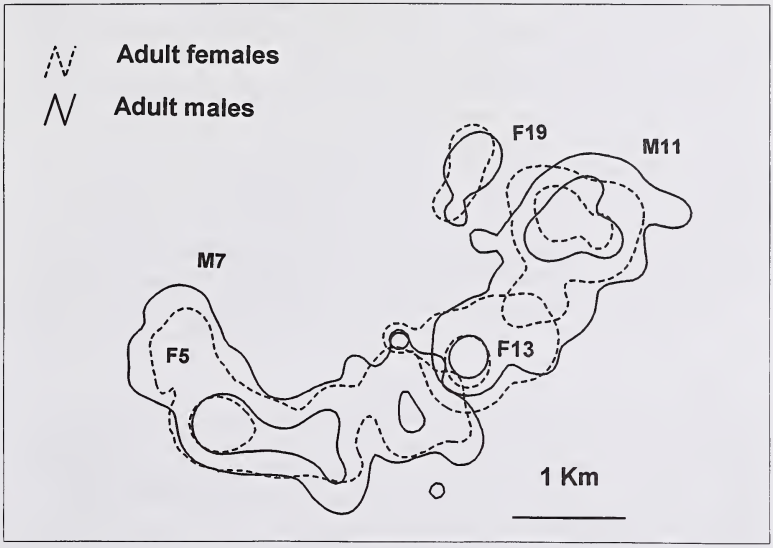

Figure 1. Home ranges of 2 male/female nuclei of stone martens (M7/F5, M11/F13-F19), as calculated by the kernel estimator (outer boundary: 95% probability contour line; inner boundary: 50% probability contour line).

M11's home range overlapped those of two females, F13 and F19; M11 and F13 were tracked simultaneously for 369 days, whereas M11 and F19 were tracked simultaneously for 72 days, until F19 died. Thus, 2 nuclei were identified: 1 of 1 male and 1 female (M7-F5), and 1 of 1 male and 2 females (M11-F13-F19). In spring 1993, M7 enlarged its home range to include part of that of M11; during this period M7 and F13 were often associated, and as a result we consider them as a mating pair. At this time M11 reduced its home range to the area used by F19. After about 6 months the home ranges returned to their original sizes. Considering the 6-month period of association between M7 and F13, we obtained a total sample of 4 mating pairs (M7-F5, M7-F13, M11-F13, M11-F19).

Home ranges were stable from year to year (3 individuals were tracked for more than 2 years). When an adult died, a neighbor of the same sex rapidly (within 1-2 weeks) occupied, partially or completely, the vacant territory (n = 3, 2 males and 1 female).

Analysis of internal use of home ranges by means of the kernel estimator showed marked coincident use of space by mating pairs in both the 1 male/

1 female and 1 male/2 females nuclei (Fig.1). Spatial niche overlap between adult males and adult females was high (range = 0.467-0.690), but there was little overlap within sexes (range = 0.003-0.215). The difference in spatial niche overlap between the 2 categories (same sex, different sexes) was significant (Z = -3.1; P = 0.002). Overlap was variable between adults and young (range = 0.071-0.667), but was always high (>0.49) when young were <6 months old. Spatial niche overlap was not correlated with total home range overlap (same sex: df = 6, F = 1.41, P = 0.28; different sexes: df = 8, F = 1.50, P = 0.25). Individuals of different sex showed high spatial niche overlap even when total home ranges overlapped only slightly. In contrast, adults of the same sex showed little spatial niche overlap even when total home ranges overlapped to a large extent (Fig. 2).

Home-range size did not show significant seasonal variations in either males (χ^2 = 8.44, P = 0.13) or females (χ^2 = 6.26, P = 0.28), and variation did not

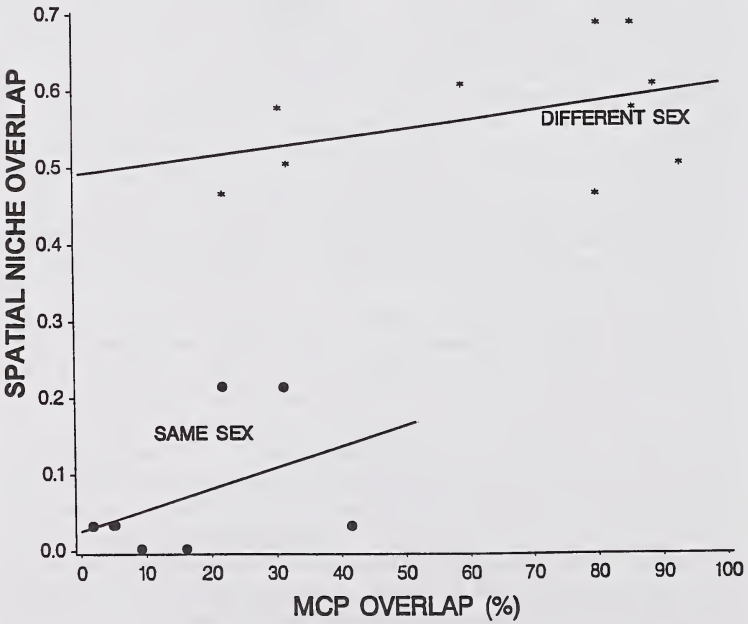

Figure 2. Correlation between spatial niche overlap (Horn's index) and home range overlap (minimum convex polygon) calculated for pairs of adults of the same sex and of different sexes. For each pair, only periods of tracking of both animals are considered.

differ significantly between males and females ($Z = 0.23$, $P = 0.82$; Fig. 3). Association of adult males and females in the day-resting sites was frequent (30.14% of days, 4 pairs considered; 438 days of contemporary monitoring of both individuals). For 2 pairs in which reproduction was proven (re-captured while lactating), we found a peak of male presence at the resting site during the lactation period when cubs were present (Fig. 4). We twice observed the adult male associated with young in their first months of life (May to July). In 1 mating pair that was simultaneously tracked during reproduction, we recorded a peak in the male's activity (distance moved in 24 h, as estimated by all-night observations) when the female was lactating and had markedly reduced her activity (Fig. 5); in such cases the male was observed going to the resting site more than once in 24 h.

Discussion

The studied population showed a clear territorial pattern. Our data confirm the intrasexual territoriality model for the stone marten, and quick colonization of vacant areas seems to indicate an active defence of territories by adults.

The marked coincident use of space (high spatial niche overlap) between males and females with overlapping home ranges is inconsistent with the hypothesis of spatial segregation between sexes. Males' home ranges were stable

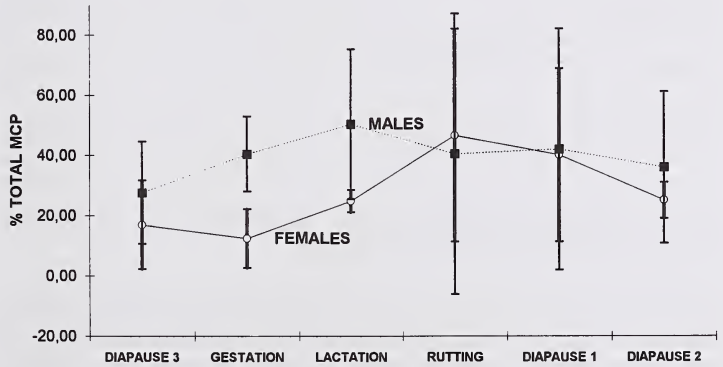

Figure 3. Variation of seasonal home ranges (minimum convex polygon), measured as the percentage (mean ± SD) of the total home range (6 adult males: 37 seasonal MCPs; 3 adult females: 18 seasonal MCPs). Two-month seasons were defined on the basis of the reproductive cycle of the species (see text).

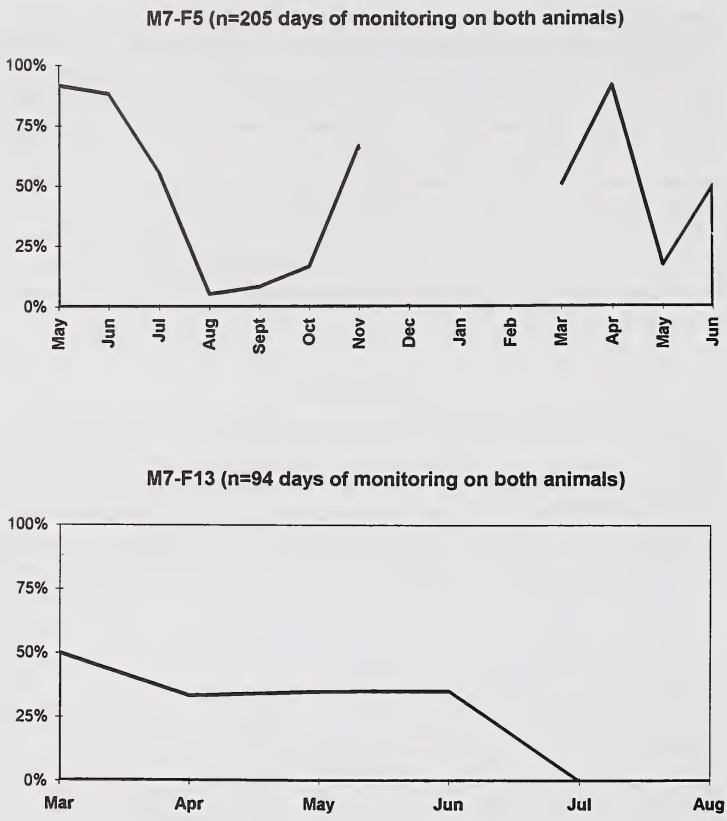

Figure 4. Simultaneous presence of a mating pair in day-resting sites (percentage of days that both individuals were monitored).

throughout the seasons. Surprisingly, male home-range size was larger (although not significantly) in the lactating season than in the mating season. Similar patterns were recorded by Herrmann (1994). These results appear to contradict the hypothesis of a roaming strategy, which is predicted in the absence of male parental investment (Sandell 1989). On the contrary, male stone martens in our study appeared to adopt a mating strategy based on maintaining a stable territory, thus monopolizing 1 or more females. This strategy does not appear to be

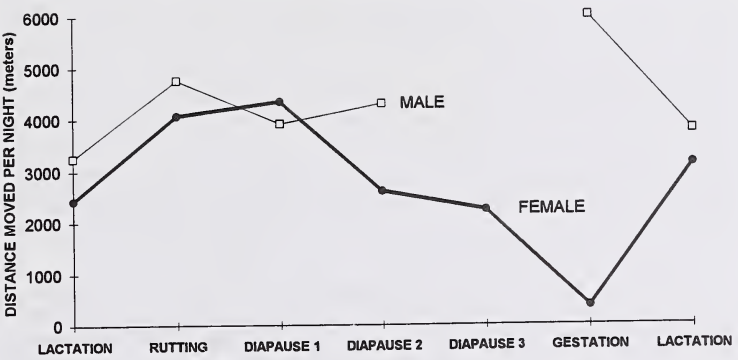

Figure 5. Distance moved per night by a mating pair (M7/F5) that reproduced during the research period. The distance was calculated by connecting successive locations recorded during continuous tracking sessions (radio locations every 15 min).

consistent with either the monoestrism of the species or the low density of females, which is probably not much higher than that of males (Sandell 1989).

These 2 unexpected results indicate an extended relationship within the mating pair and suggest that some benefit must arise from such an association. Familiarity within mating units could explain the above spacing patterns; it probably increases the possibility of mating and reduces the risk of intraspecific aggression. Nevertheless, frequent association of the male with young during the lactation period and the following months, and the increase in the male's activity when the female has reduced her movements, appear consistent with the hypothesis of a male parental investment through food provisioning, defence against conspecifics, defence from predators, and training of young. An increase in the male's activity in coincidence with a reduction in the females' movements was also recorded by Balharry (1993) for the Eurasian pine marten (*M. martes*).

Although no direct data on male parental care are available for stone martens or related species, several inferences can be made from this and other studies. A necessary, but insufficient, condition for male parental care is certainty of paternity (Kleiman and Malcolm 1981); the substantial stability of territories of stone martens, as confirmed by other authors (Skirnisson 1986, Müskens et al. 1989, Herrmann 1994), is evidence of a high likelihood that the male present in the territory of a female at parturition is the father. An indication of possible cooperation within the mating pair was recorded by Krott (1973) for Eurasian pine martens; through studying a hand-raised female that mated with a wild male, the

author observed the male bringing food to the female. This is consistent with the hypothesis of male cooperation through food provision. The same author recorded the simultaneous presence of both sexes in the reproduction den; association of a male and female stone marten in day-resting sites has also been reported by Müskens et al. (1989) and Skirnisson (1986). Moreover, several studies indicated an increase in male secondary characters of territoriality after parturition: increase of testosterone level in pine martens (Balharry 1993), and enlargement of testes (Madsen and Rasmussen 1985) and territories (Herrmann 1989) in stone martens. These results appear consistent with the hypothesis of active defence of cubs by the male hypothesized for the pine marten by Balharry (1993).

These factors support, but do not prove, the hypothesis of male parental behavior. Such behavior would increase survival of the young, and thus balance the reduced probability of mating with more than 1 female, which occurs when males abandon a roaming strategy. Thus, the male's parental investment could represent a key factor in the social ecology of the stone marten, significantly affecting its spacing patterns and social system. However, the variable number of females per male indicates that the male's cooperation may not be essential for successful rearing of offspring (Bekoff et al. 1984).

We therefore propose a paternal-investment polygyny model for the species that differs from other polygynic systems for the attachment within the mating pair; such a relationship affects the spacing patterns of adults, limits the male: female ratio, and could increase the survival of young. We speculate that paternal-investment polygyny can develop only when intraspecific competition is limited, as appears to be the case in the stone marten, which shows high adaptability in diet, habitat selection patterns and foraging strategies (Clevenger 1994, Genovesi et al. 1996). Tolerance within the mating unit would be much less advantageous for predators feeding on only vertebrates, as is the case with most felids.

We suggest that this model of paternal-investment polygyny should be considered intermediate between polygamy, as shown by most solitary carnivores, and facultative monogamy (*sensu* Kleiman 1977), as described for the maned wolf, *Chrysocyon brachyurus* (Dietz 1984). If this model is confirmed, the mating system within Carnivora could then be described as a gradient between polygamy and the more complex social interactions shown by canids, which are characterized by the critical need for male investment in the rearing and survival of offspring (Moehlman 1989).

In order to confirm the paternal-investment polygyny model for the stone marten, more observations are required on the males' parental behavior. The differential survival of young when the male is removed from a nucleus should also be investigated. Finally, the survival of offspring of nuclei of 1 male/1 female (higher male investment), should be compared to that of nuclei of 1 male/more than 1 female (lower male investment).

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Part III

Habitat Characteristics and Utilization

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HOME-RANGE SIZE AND FIDELITY OF AMERICAN MARTENS IN THE ROCKY MOUNTAINS OF SOUTHERN WYOMING

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Abstract: Using telemetry data from radio-collared American martens (*Martes americana*) collected between 1985 and 1995 in south-central Wyoming, USA, we calculated home-range areas using the minimum convex polygon (MCP) and adaptive kernel (ADK) methods for individuals that were relocated at least 30 times per season (summer and winter, broadly defined). For animals that were radio-collared for at least 4 seasons, we calculated home-range fidelity as the percentage of an animal's home range during one season that overlapped with its home range during the previous season. We also calculated fidelity to the home range of the same season in the previous year. Mean home-range size (95% MCP) for adult females was 669 ha for summer and 592 ha for winter. Mean home-range size for adult males was 1820 ha in summer and 1459 ha in winter. Home-range sizes measured by the 95% ADK were higher. Marten exhibited high home-range fidelity to the previous season and to the same season of the previous year. Large shifts in home ranges were rare.

Introduction

Maintaining a home range may afford an animal a number of benefits. As an animal becomes more familiar with an area it can better assess the distribution of prey and the availability of resting sites and refuges (Burt 1943, Davis et al. 1948). A home range may help carnivores secure access to mates (Powell 1994). Given these advantages, fidelity to an area over seasons and years should be advantageous as long as the area continues to provide adequate resources. Loss of habitat may force American martens (*Martes americana*) to enlarge or move their home range to encompass more suitable habitat.

An observer must first define home-range boundaries to measure changes in home-range size or fidelity. The minimum convex polygon method (called the "minimum home range" by Mohr 1947) has the advantage of being simple to define and conceptualize, and allows for comparison to previous marten home-range studies (e.g., Buskirk and McDonald 1989, Powell 1994). However, Burt (1943) noted that connecting outlying points may be misleading and actual home ranges probably have amoeboid outlines. Worton (1989) promoted kernel methods for home range studies. Kernel methods use all the locational data (not just the extremes) and can produce irregular shapes and multiple polygons (see Worton 1995). Powell (1993) recommended kernel methods be adopted for *Martes* research.

This study on American marten was initiated in 1985 as part of a long-term study on the effects of timber harvest on wildlife (Raphael 1987). Base-line information on natural variation in home-range size and fidelity is needed to understand the potential effects of disturbance. The objectives of this paper are: (1) to quantify marten home-range sizes in south-central Wyoming by season and by gender; (2) to measure individual martens' degree of fidelity to their home ranges over multiple seasons including periods of timber harvest; and (3) to compare the effects of the home-range estimator (minimum convex polygon versus adaptive kernel) on these measurements.

Study Area

The center of the study area lies at about 41° 3' N latitude and 106° 45' W longitude in the Sierra Madre Range of the Central Rocky Mountains. The study area was initially defined by the boundaries of a water yield augmentation study (see Bevenger and Troendle 1987) and encompassed 2 watersheds (28 km^2 in total) in the Medicine Bow National Forest in south-central Wyoming, USA. More than 200 small (less than 8 ha) clear-cuts were created in the eastern watershed (Coon Creek) from August 1990 through October 1992 for the water yield study. However, due to dispersal of collared martens and the extent of their home ranges, the study area was expanded to about 270 km^2 (Fig. 1) and includes a portion of the Routt National Forest in northern Colorado. Forest types intermingle and consist predominantly of spruce/fir (*Picea engelmannii* and *Abies lasiocarpa*) and lodgepole pine (*Pinus contorta*). Clear-cuts, meadows (wet and dry), and rock outcrops are interspersed throughout the area. Mean annual precipitation between May 1983 and December 1992 in the Coon Creek and adjacent watershed was 87 cm. Snow cover was present from at least October 1 though May 31 every year. Mean monthly temperatures over the study period ranged from -10.6°C in January to 12.9°C in July.

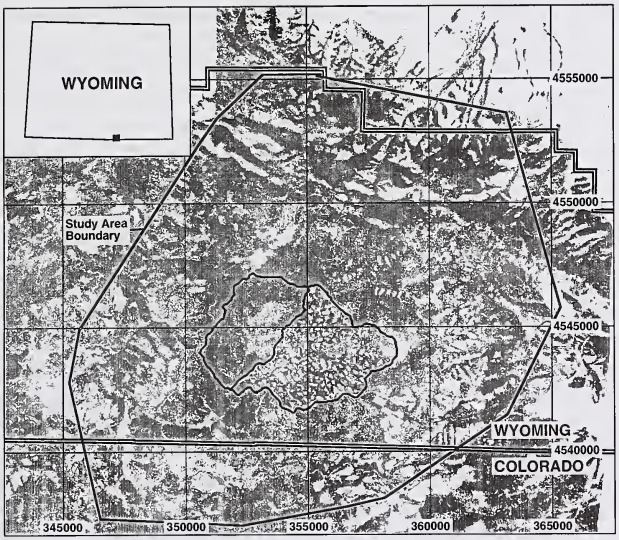

Figure 1. The study area, as defined by a minimum convex polygon around all marten telemetry locations in the area, in south-central Wyoming and an adjacent portion of Colorado. The double line indicates the Medicine Bow National Forest boundary that, along the southern border, coincides with the Wyoming-Colorado border. The polygons in the center of the map indicate the 2 watersheds of the original study area. The map is shaded to illustrate forested areas (gray) versus non-forested areas (white). The small clear-cuts in the eastern Coon Creek watershed were created between late 1990 and late 1992. A Universal Transverse Mercator (Zone 13) grid with a spacing of 5 km is superimposed on the map. The inset in the upper left shows the location of the study area (solid black rectangle) in Wyoming.

Methods

We attempted to locate all radio-collared martens with aerial telemetry at least twice weekly except for a few months when funding was insufficient. Animal locations that were obtained from aerial and ground telemetry were recorded on topographic maps (scale 1:24000) and digitized using a 100-m Universal Transverse Mercator (UTM) grid. The location data for each animal were divided into 2 seasons that we defined by snow cover (June 1 through September 30

as summer, and October 1 though May 31 as winter) and by year. The designation of a winter season was based on the year in which it began. These subsets of data will be referred to as animal-seasons.

We estimated home-range size for each animal-season using the minimum convex polygon (MCP) method (Mohr 1947) and adaptive kernel (ADK) method (see Worton 1989). We used the 95% contour for both estimators to minimize the effect of outliers. The 95% MCP was calculated using the University of Idaho HOME RANGE program (Ackerman et al. 1990). The 95% ADK home-range polygons were determined using the program CALHOME (Kie et al. 1996) with a constant grid size of 200 m and a bandwidth assigned by the program (using the method of Worton 1989). We summarized the home-range sizes by sex and season for adults with at least 30 relocations per season. Statistical comparisons of home-range sizes by sex and by season were made with a *t*-test. We used a pair-wise comparison (paired *t*-test) to determine if the MCP and ADK methods yielded different-sized home ranges for each animal-season.

Only martens that were tracked for at least 4 seasons as adults were included in the fidelity analysis. This criterion reduced the number of animals in the fidelity analysis from the 96 animals collared to date to only 8 (5 females: F29, F37, F49, F53, and F60; and 3 males: M26, M31, and M35). The results of the home-range programs were converted to a vector format acceptable for the public-domain geographic information system (GIS) GRASS (USA-CERL 1991). The GRASS vectors were converted to raster format at a resolution of 30 m. We determined home-range fidelity in GRASS by calculating the percentage of a seasonal home-range area that included the previous seasonal home-range area (where sample size was at least 30 relocations). The periods considered were between consecutive seasons (i.e., winter to the previous summer and summer to the previous winter) and between the same season in consecutive years (i.e., winter to the previous winter and summer to the previous summer). We determined fidelity for both measures of home range (95% MCP and 95% ADK).

To establish the percentage overlap that can be expected when an animal's home range is constant, we selected 1 data set in which there were 69 relocations in 1 season (M35, winter 1990). From these data we used a bootstrap procedure, which randomly selects 30 relocations (with replacement) from the original pool of relocations as input for the program HOME RANGE, to establish a 95% MCP convex polygon. We compared each polygon to another randomly selected polygon and calculated the percentage overlap. These steps were repeated 1000 times. From plots of the variance of percentage overlap and of home-range size as a function of sample size, we determined that 1000 repetitions were more than adequate because variances stabilized between 500 and 600 repetitions. Although the locations were taken from the same pool, the home-range areas ranged from 558 ha to 1561 ha. The mean overlap with the standard polygon

was 82.8% (SE = 0.34) and 95% of the values were greater than 65%. Therefore, we considered fidelity values above 65% to represent high fidelity, meaning that we are unable to detect a shift in home range.

Results

Home-Range Size

Results from the HOME RANGE program indicated that within animal-seasons the data were not autocorrelated and were generally uniformly distributed. Seasonal home-range area (95% MCP) of adult males varied from 460 to 3891 ha in winter and from 779 to 2718 ha in summer. The distribution of male home-range sizes for winter was skewed right with a few very large values. The males represented by those large values did not appear to be transients because they continued to use the same area in subsequent seasons. Female 95% MCP areas had a narrower range: from 266 to 1222 ha in summer and from 330 to 1053 ha in winter. Mean home-range size of males was much greater than of females ($P < 0.0001$; Table 1). For each animal-season the 95% ADK home-range areas were greater than those of the 95% MCP ($P < 0.0001$). The within-sex differences between summer and winter home-range sizes were not significant (all $P > 0.2$).

Home-range size, regardless of estimator used, was quite variable within and among animals over seasons and years for both females and males (Figs. 2 and 3, respectively). There was no evidence to indicate that juveniles range over a large area before settling into a defensible territory. Individuals' home-range

Table 1. Summary statistics for adult marten home-range sizes (ha) by gender and season based on the 95% minimum convex polygon (MCP) and 95% adaptive kernel (ADK) methods. Only adult martens that were relocated at least 30 times each season were included. Note that "*n*" refers to the number of animal-seasons that were used in the calculation of means and SE. Some animals are over-represented in these means.

		Number of animals	*n*	95% MCP (ha) Mean	SE	95% ADK (ha) Mean	SE
Females							
	Summer	7	16	669	67	1070	109
	Winter	8	19	592	37	912	58
Males							
	Summer	8	14	1820	153	3112	302
	Winter	13	21	1459	210	2564	327

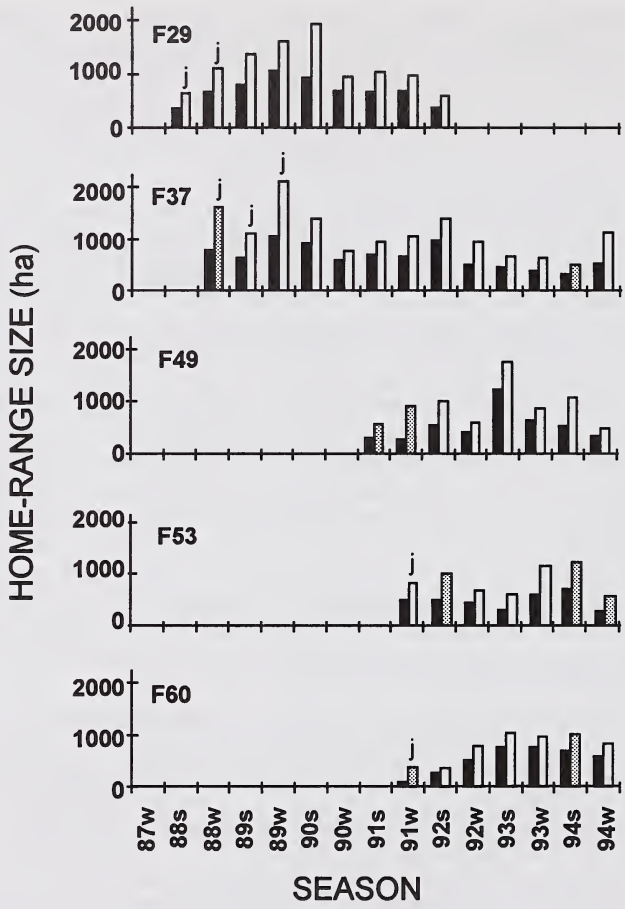

Figure 2. Female summer and winter home-range sizes (ha) as determined by the 95% minimum convex polygon (black columns) and adaptive kernel (white columns, or gray columns if the sample size for that animal-season was insufficient) methods for F29, F37, F49, F53, and F60. The superscript "j" above a pair of columns indicates the animal was a juvenile in that season. In naming seasons, the numbers refer to the year and the letters "w" and "s" refer to winter or summer, respectively.

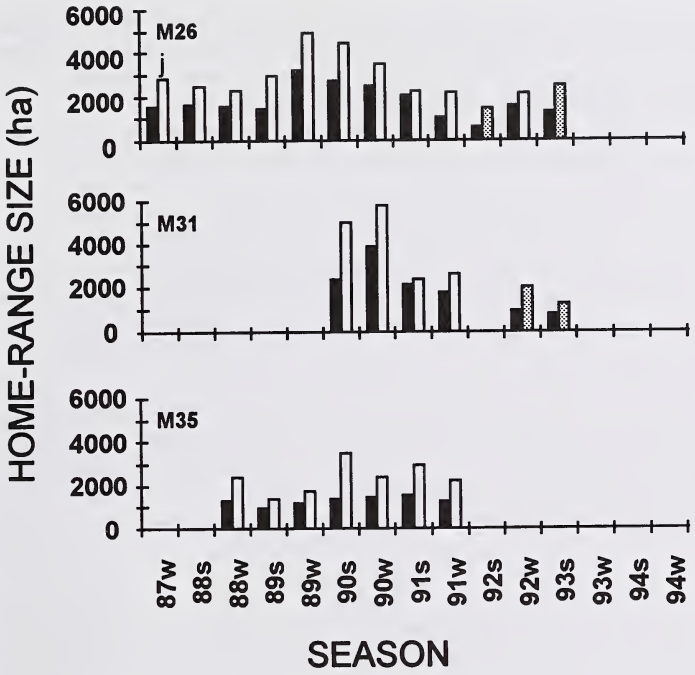

Figure 3. Male summer and winter home-range sizes (ha) as determined by the 95% minimum convex polygon (black columns) and adaptive kernel (white columns, or gray columns if the sample size for that animal-season was insufficient) methods for M26, M31, and M35. The superscript "j" above a pair of columns indicates the animal was a juvenile in that season. In naming seasons, the numbers refer to the year and the letters "w" and "s" refer to winter or summer, respectively.

sizes varied with no apparent pattern relative to age, season, or year, including the years of timber harvesting (1990-1992).

Fidelity

Estimates of home-range overlap based on 95% MCP and 95% ADK gave similar results (Table 2). In only 8 of 52 pairs did the MCP and ADK overlap yield a different interpretation based on our criterion of 65% and above

representing high fidelity. In all but 1 pair, the fidelity value from the MCP was within 15% of that from the ADK. Despite differences in home-range size, most animals kept at least part of the same home range over the period studied. No animals completely abandoned a home range in 1 or 2 seasons.

F29 showed lower home-range fidelity as a juvenile, but appeared to settle into an area just before reaching adulthood. Her home-range fidelity appeared to be lower again from winter 1989 through the end of summer 1990. F37 exhibited high fidelity through most of 12 seasons, except moderate fidelity indices as a juvenile in winter 1989, and summer 1992 (the last season of logging). Fidelity values for F49, F53 and F60 indicated moderate home-range shifts in 1 or 2 seasons.

M26 made a gradual shift in home range in the first 2 seasons of its adulthood (summer and winter 1989) and then fidelity remained relatively high. M31's home range shifted slightly in winter 1990 but was constant through winter 1991. M35 exhibited high fidelity in 4 of 6 seasons.

The annual seasonal fidelity (the percentage of a seasonal home range that includes the home range of the same season in the previous year) revealed a similar trend to fidelity to the previous season. However, the values were usually lower (about 5%). The lowest fidelity value (24%) was for F60 in summer 1993 compared to summer 1992.

Discussion

Presumably, animal home-range sizes shift in response to resource availability and to the activities of neighboring martens (Powell 1994). In this study each animal's home-range size varied greatly over time. The range of this variation was greater than that found in the bootstrap test discussed above. Unfortunately, this variability reduces the power for detecting changes in home-range size due to disturbance. Logging of the Coon Creek watershed began in 1990, but was not widespread until late in 1991. Females 29, 37, and 53 and Males 26 and 35 all occupied some part of the Coon Creek watershed during their life span. However, F29 and M35 died during the logging period, and F53 became an adult during that period. Thus, only 1 female and 1 male in these analyses spanned the time before and after logging. Trends in their home-range sizes over time do not support the hypothesis that home-range size increases in response to habitat loss. However, since the scale of the disturbance was small relative to the size of marten home ranges that hypothesis cannot be tested directly. Prey abundance may be more important in determining home-range size (Thompson and Colgan 1987).

Variation in home-range size among these martens was large, perhaps reflecting relative dominance or habitat quality. The male martens in our study area had extremely large home ranges. The mean 95% MCP for males was most similar

Table 2. Home-range fidelity (percentage of the seasonal home range that includes the home range of the previous season) for martens tracked for at least 4 seasons. M refers to the overlap of 95% MCP home ranges and A refers to the overlap of 95% ADK home ranges. Underlined values represent seasons when the animal was less than 2 years of age. An asterisk indicates that we had an insufficient sample size (< 30) in the previous season for an adequate comparison.

Animal:	F29		F37		F49		F53		F60		M26		M31		M35	
Season:	M	A	M	A	M	A	M	A	M	A	M	A	M	A	M	A
1988 Summer											69	80				
1988 Winter	43	49									81	75				
1989 Summer	79	79	77	85							43	50			94	85
1989 Winter	59	74	59	52							45	54			58	56
1990 Summer	48	61	78	96							87	93			73	50
1990 Winter	85	95	94	99							85	81	56	70	76	94
1991 Summer	72	60	80	73							79	92	95	93	76	72
1991 Winter	71	73	76	72	*	*					77	62	87	69	93	91
1992 Summer	100	94	66	64	*	*	82	74	*	*	83	94				
1992 Winter			100	90	90	94	*	*	45	44	*	*				
1993 Summer			75	93	31	33	96	87	55	67	97	73				
1993 Winter			89	81	87	92	33	47	82	90						
1994 Summer			81	88	73	59	59	69	75	68						
1994 Winter			*	*	97	100	99	97								

to male home ranges in Minnesota (minimum polygon, Mech and Rogers 1977), Newfoundland (Bateman 1986; Bissonette et al. 1988, as reported in Buskirk and McDonald 1989), and Northwest Territories (Latour et al. 1994). Several males had seasonal home ranges greater than 3000 ha, which is larger than any reported in the review by Buskirk and McDonald (1989), and 75% of the summer and winter home ranges were above 1425 ha and 778 ha, respectively. Our estimates of female home ranges (mean and maximum 95% MCP) were within the range of those compiled by Buskirk and McDonald (1989) and most similar to home ranges for female marten in Alaska and Newfoundland.

For most animal-seasons in this study, the bivariate distribution of location data was uniform, thus MCP is a reasonable model (Samuel and Garton 1985). The ADK method results in large home ranges relative to MCP and it indicates a great deal of overlap between animals. Although smaller contours of the ADK may be appropriate for studying habitat utilization, we believe that MCP is more suitable for defining territorial boundaries. For a territorial animal such as a

marten (Wynne and Sherburne 1984, Thompson and Colgan 1987; Katnik et al. 1994), the boundary between 2 males may truly approximate a line, with virtually no overlap. The ADK area is dependent on several variables used in the algorithm including the grid size and the bandwidth. The choices of variables used in this analysis could be modified to yield smaller and perhaps more accurate 95% ADK areas. Worton (1995) made suggestions on better ways of choosing bandwidths.

The choice of home-range estimator did not have much effect on the interpretation of home-range fidelity. Moderate home-range shifts were observed, but martens never relocated to a totally new area over 1 or 2 seasons. Our analysis could have missed gradual shifts leading to abandonment of an area after 3 seasons, but home-range maps showed this generally was not the case. Although marten home-range size varied, the position of the home range on the landscape varied little. All animals except M26 retained some common area among all seasons. M26's home range (95% MCP) during summer 1989 did not overlap with those of 3 seasons (winters 1991, 1992 and summer 1993). Nonetheless, the 95% ADK polygons did overlap.

The 8 adult martens chosen for the fidelity analysis were relatively long-lived (only animals that lived at least 2 years beyond sexual maturity were included). All the females successfully reared at least 1 litter. We assume M26 and M35 sired litters. We never caught a female in M31's range so we cannot speculate that it sired kits. The female with the most consistently high home-range fidelity (F37) also lived the longest. High home-range fidelity may be a crucial factor for marten survival and reproductive success.

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DEN AND REST-SITE CHARACTERISTICS OF AMERICAN MARTEN AND FISHER IN NORTHERN WISCONSIN

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Abstract: American martens (*Martes americana*) and fishers (*M. pennanti*) are reported to use mature or old-growth forests to meet some or all of their needs. Coarse woody debris (CWD) and dead and down woody material (DDWM) are components of these forests that provide martens with resting sites for thermal cover, hunting locations and maternal dens. During the winter of 1993-1994 we located 32 marten resting sites. Of these rest sites, 66% (21) were underground and 6.2% (2) were in standing trees. Nearly 67% (14) of the underground rest sites were in tip-up mounds created by the root mass of fallen trees or other mound formations. The total volume of CWD, the volume and number of downed logs (>7.5 cm diameter) and the number of rotten tip-up mounds were significantly greater in winter marten rest-site locations compared to measures on randomly placed plots. During the spring we located 7 female marten dens and 12 male marten resting sites; 85% of the maternal dens and 93% of the male resting sites were in standing trees, and no underground sites were used. Fourteen fisher resting and den sites were located in both seasons. Most fisher sites were in standing trees (57%) or directly associated with CWD or DDWM (28%), while only two underground fisher sites were found. No distinct patterns were observed in fisher rest-site characteristics except that all maternal dens were located in standing live trees. No differences in the volume of DDWM or the number of logs, snags, stumps or tip-ups were detected for fisher resting sites or dens compared to random plots. Most dens or rest sites of both species were located in upland timber types, especially northern hardwoods and upland conifers. There were no differences in diameters, heights or location and size of openings between marten

and fisher den trees. Martens and fishers use different types of rest sites during winter months but use similar types of rest sites and maternal dens during spring.

Introduction

Forest structure, especially coarse woody debris (CWD), is proposed as an important factor in determining both fisher (*Martes pennanti*) and American marten (*M. americana*) distribution and habitat use (for marten, Buskirk 1984, Harmon et al. 1986, Spencer 1987, Buskirk et al. 1989; for fisher, Coulter 1966, Powell 1977, Raphael 1984, Arthur et al. 1989, Thomasma et al. 1991, Buskirk and Powell 1994). Both forest structure and woody debris increase as the age of the forest stand increases (Thomas et al. 1979). Older forests tend to have more complex vertical and horizontal structures because disturbance regimes (e.g., gap disturbances) and other processes, such as natural mortality, associated with older forests promote these structures (Lorimer 1989, Hunter 1990, Muller and Liu 1991).

The effect of complex forest structure may be observed at the broader habitat selection scale. Animals may choose home ranges and may select habitats within their home ranges based on broad differences in forest structure. Marten habitat use has been tied to differences in habitat structure rather than species composition over many portions of their range (Buskirk and Ruggiero 1994). Fishers also have been reported to prefer forested stands with a high degree of canopy closure and physical structure (Powell and Zielinski 1994). Forest structure may also operate at a more site-specific location. Rather than determining broad scale habitat use or preferences, these structures could determine site-specific habitat use by fishers and martens, such as den or rest-site selection (Arthur 1987; Paragi 1990; Buskirk and Ruggiero 1994) or the use of subnivean access points (Corn and Raphael 1992).

We studied the role of CWD in the upper Great Lakes region primarily because these ecosystem elements and the role they play in determining fisher and marten habitat use in this region are poorly understood. Most published information concerning the effect of forest structure on habitat selection comes from the western states and Canada. The role of forest structure and woody materials on home range and habitat selection in the upper Great Lakes was studied by Wright and Gilbert (unpubl. data). Here we consider the role these structures play in den and rest-site selection. Our objectives were to locate and describe marten and fisher dens and rest sites. We were especially interested if CWD and dead and down woody material (DDWM) are important factors to both species in determining selection of dens and rest sites, and if this woody material is important in both winter and spring.

We hypothesized that the amounts of DDWM and volumes of CWD at marten and fisher dens and rest sites differ from those found randomly, but are the same at winter rest sites and at spring maternal dens.

Study Area

The study area was located in the Eagle River District of the Nicolet National Forest, Forest County, Wisconsin. Topography is typified by northeast-southwest parallel glacial drumlins separated by wet lowlands. The drumlin soils are well- to moderately well-drained silt loams. Soils between drumlins are moderate to poorly drained, medium silt to fine sandy loams. The climate includes long winters and short cool summers. Average annual temperature is 5°C ranging from a mean of -13°C in January to 19°C in July. Average annual precipitation is 78.2 cm.

The region was subjected to extensive logging and fire in the early 1900's, and logging continues today. The result is a mosaic of cover types differing in composition, structure and age. The mixed hardwood forests are most common throughout the study area. These forests are dominated by sugar maple (*Acer saccharum*), American basswood (*Tilia americana*), paper birch (*Betula papyrifera*), white ash *(Fraximus americana*), and red oak (*Quercus rubra*). The lowland areas are dominated by black spruce (*Picea mariana*), white cedar (*Thuja occidentalis*) and tamarack (*Larix laricina*). Scattered stands of red pine (*Pinus resinosa*) and upland conifers also exist on the well-drained, sandy soils. Upland conifers are dominated by large diameter eastern hemlock (*Tsuga canadensis*) and white pine (*Pinus strobus*) which often form a "super" canopy over the mixed hardwoods. An extensive road network exists in the area. There are no year-round residents, but there are a small number of private landholdings that have cabins, which are used seasonally.

Methods

Fishers and martens were captured using box traps (Tomahawk Trap Co., Tomahawk, Wisconsin) baited with meat scraps and a commercial lure during the fall and winter of 1992 and 1993. All animals were immobilized with ketamine HCL mixed 10:1 with xylazine (0.1 mg/kg body wt.). Adults were fitted with radio-collars (Advanced Telemetry Systems, Isanti, Minnesota).

Animals were located up to 2 times per day with a truck-mounted, 5-element Yagi directional antenna (Telonics, Mesa, Arizona). When bouts of inactivity exceeded 6 hours in the same location, dens or rest sites were located by walking in on the animals using a hand-held antenna system. Sites were located throughout the

winter and into the spring. All sites were flagged in the field and marked on a map for easy relocation in the spring and summer.

After snow melt, all sites were revisited and described including habitat type, den or rest-site type, number of entrances, entry location and size of entry. Number of snags (standing dead trees greater than 2 m in height), logs (dead and downed trees greater than 7.5 cm in diameter), stumps (remains after the harvest of a tree) and tip-up mounds (the root mass of a fallen tree) were counted in 0.2 ha circular plots.

The 4 size classes of DDWM were defined as small branches less than 0.5 cm in diameter, medium branches between 0.5 and 2.5 cm in diameter, larger branches or small logs between 2.5 and 7.5 cm in diameter, and large logs greater than 7.5 cm in diameter. Decay classes followed a collapsed version of decay classes presented by Maser et al. (1979). New logs were equivalent to class 1 logs presented by Maser et al. (1979), that is, logs with bark and small branches present. Sound logs were those with no small branches and with a hard texture (classes 2 and 3 in Maser et al. 1979). Rotten logs had no bark and soft, decayed wood (classes 4 and 5 in Maser et al. 1979). Snags, stumps and tip-ups were classified in the same way. Volumes of DDWM were measured following a modified technique described by Brown (1974). We modified Brown's calculations to yield estimates of the volume of woody material in 4 size classes and the volume of logs in 3 decay classes. Mean values used in the calculation of volume for the 4 classes of DDWM were 0.25, 1.5, 5.0, and 14.5 cm, respectively.

We quantified CWD and DDWM on 625 randomly placed plots, stratified by cover type and in 1 plot centered on each den or rest site. Random plots were located by over-laying a grid on aerial photos of forest stands and randomly selecting grid intersections within each stand type. The number of random plots in each forest cover type was proportionate to the area of the cover type in the study area. The 625 random plots were sufficient to reduce the coefficient of variation of each measure to less than 10%.

We compared measures of CWD (number of snags, logs, stumps and tip-ups) and volumes of DDWM between random plots and those plots located at dens and rest sites. *T*-tests (Zar 1984) were used to compare between measures made at dens or rest sites and measures made on randomly located plots. A significance level of 0.05 was used for all tests.

Results

We captured and radio-collared 18 martens and 8 fishers during the study. Rest sites and maternal dens were located for 12 martens and 6 fishers. We located 32 marten winter rest sites and 19 marten spring sites including 7 maternal dens. We also located 8 fisher winter rest sites and 6 fisher spring sites including 4 maternal

dens. Most sites (63% and 67% for martens and fishers, respectively) were located during winter months and selection was probably based on thermal cover needs. We had fewer fishers with radio collars and fishers did not seem to rest in one spot long enough to permit a positive location of resting sites.

Of the 32 winter marten rest sites, 30 were either underground (in rock piles, excavated holes or tip-up mounds) or under woody material; only 2 were located in standing live trees or snags (Table 1). Fourteen (66%) of the underground winter rest sites were in tip-up mounds. The majority of rest sites found under woody material were in or under decayed root masses. In spring, 6 of the 7 marten maternal dens and 10 of the 12 rest sites were in standing trees greater than 50 cm in diameter (mean = 55.9 cm), whereas only 3 spring marten dens or rest sites were associated with dead and down woody material and none were located underground.

In winter, fisher rest sites were underground, under woody material or in standing trees. There was no clear preference demonstrated for any type of rest site. No male rest site was located in the spring, whereas 5 of the 6 female fisher dens located in the spring were in standing live trees of at least 52 cm in diameter (mean = 60.9 cm).

Table 1. Number of winter and spring American marten dens and rest sites located under ground, under slash, and in standing trees in northern Wisconsin, 1992-1993.

	Winter		Spring	
	Male	Female	Male	Female
Subterranean	5	1	0	0
Tip-up mounds[a]	12	2	0	0
Under rocks	1	0	0	0
Total underground	18	3	0	0
Stumps	0	4	1	0
Under tree	1	3	0	0
Under slash	1	0	0	0
Hollow log	0	0	1	1
Total under CWD[b]	2	7	2	1
Live trees	2	0	8	5
Snags	0	0	2	1
Total in trees	2	0	10	6

[a] Tip-up mounds - root masses of fallen trees.

[b] CWD - coarse woody debris.

Table 2. Percent (number) of winter and spring dens and rest sites selected by American martens and fishers in 5 habitat types in northern Wisconsin, 1992-1993.

	Percent of Study Area	Percent (#) of Marten Dens		Percent (#) of Fisher Dens	
		Winter	Spring	Winter	Spring
Upland Conifer	10.1	28.1 (9)	10.5 (2)	37.5 (3)	0
Mixed upland Conifer/ Hardwoods	17.6	0	21.1 (4)	0	0
Upland Hardwoods	42.7	65.6 (21)	68.4 (13)	62.5 (5)	75.0 (3)
Swamp Conifer	20.8	6.3 (2)	0	0	0
Non-forested	8.8	0	0	0	25.0 (1)

Most den and resting sites for both species were located in upland cover types, with upland hardwoods and upland conifers containing 56 of the 64 sites (Table 2). These 2 cover types constituted 54% of the study area but contained 89% of the den or rest sites. Wright and Gilbert (unpublished data) determined that the area of all cover-types within the home ranges of radio marked martens and fishers on this study area was proportionate to the amount of that cover-type in the study area but den and rest sites were predominantly found in the upland cover types.

Total volume of DDWM and volume of logs (> 7.5 cm diameter) were greater at marten winter rest sites than on random plots (DDWM: $P = 0.03$, 34 df; log volume: $P = 0.04$, 35 df) (Table 3). The numbers of logs, new snags and rotten tip-ups per hectare were significantly greater at marten winter rest sites than at random plots (logs: $P = 0.02$, 36 df; new snags: $P = 0.03$, 34 df; rotten tip-ups: $P = 0.02$, 34 df) (Table 4). There were no differences in the number of logs, snags, stumps or tip-ups detected in plots around marten spring dens but the volume of class 2 DDWM was greater at spring dens than on random plots

Table 3. Volumes (m^3/ha) of dead and down woody material (DDWM) found in random plots and plots surrounding marten winter and spring dens and rest sites in northern Wisconsin, 1992-1993.

DDWM Class	Random Plots	Winter	Spring
Class 1 (<0.5 cm)	0.65	0.6	**0.8**[a]
Class 2 (0.5 - 2.5 cm)	3.7	5.1	**5.3**
Class 3 (2.5 - 7.5 cm)	7.5	12.7	6.2
Log (> 7.5 cm)	30.7	**51.1**	51.8
Total	42.5	**69.6**	63.4

[a] Volumes in bold are significantly greater than those found on random plots ($P < 0.05$).

($P < 0.01$, 17 df). No statistical comparisons were made for measures around fisher dens and rest sites because of the low sample size and consequent decrease in power.

Discussion

The role that CWD and structural diversity plays in the life history of martens has been a favorite topic in the literature (Hawley and Newby 1957, Buskirk 1984, Harmon et al. 1986, Magoun and Vernam 1986, Spencer 1987, Buskirk et al. 1989, Corn and Raphael 1992). Potential roles of woody material include predator avoidance, hunting, maternal dens (Buskirk and Ruggiero 1994), thermal protection, and subnivean access (Buskirk et al. 1989). All of these uses are associated with microhabitats (Buskirk and Ruggiero 1994). These structures are usually associated with later successional stages because the processes that form these structures are more common in late successional forests (Lorimer 1989, Hunter 1990).

Our results for winter marten resting sites support the observation that woody material is important for site-specific habitat selection. We reject the null hypothesis

Table 4. Numbers of logs, snags, stumps and root tip-ups (number/ha) found in random plots and plots surrounding marten dens and rest sites in northern Wisconsin, 1992-1993. (See text for definitions of new, sound and rotten items.)

	Random Plots	Winter	Spring
New logs	10	20	10
Sound logs	75	95	75
Rotten logs	30	35	20
Total logs	115	**150**[a]	105
New snags	20	**55**	40
Sound snags	100	55	45
Rotten snags	<5	<0.5	0
Total snags	<125	<110.5	85
New stumps	10	25	14
Sound stumps	100	100	55
Rotten stumps	135	120	120
Total stumps	245	245	189
New tip-ups	<5	<5	5
Sound tip-ups	25	20	14
Rotten tip-ups	10	**20**	16
Total tip-ups	<35	<45	35

[a] Values in bold are significantly greater than those found on random plots ($P < 0.5$).

that there is no difference in DDWM or CWD between winter marten rest sites and random plots. This woody material has been widely reported as important to site selection by martens, especially for specific features like dens and rest sites (Corn and Raphael 1992; Buskirk and Ruggiero 1994). Marten winter rest sites in this study had greater volumes of DDWM and more CWD than found randomly. These differences were due to a significantly greater volume of logs at winter rest sites and significantly more rotten tip-ups on plots surrounding marten resting

sites. Most winter rest sites were located under tip-up mounds. Tip-up mounds and logs are found together in later successional stage forests where individual trees have fallen leaving forest gaps, logs and root mounds (Hunter 1990).

We were unable to demonstrate the same relationship between DDWM and CWD for marten spring dens and resting sites. There was more woody material between 0.5 and 2.5 cm in diameter at marten sites, but we are unsure of the biological significance of this difference. The dens and rest sites were located in northern hardwoods, a later successional stage in the Great Lakes region, and mostly in large diameter trees (>50 cm diameter), both indicators of older forests, but the areas surrounding these sites contained similar amounts of CWD and volumes of DDWM as were found randomly. Thus we could not reject the null hypothesis that there is no difference in amount of woody material between spring dens or rest sites and random plots.

Unlike martens, fishers showed no selection for sites with greater amounts of CWD or volumes of woody material. There are fewer reports in the literature of associations of fisher with woody materials or structure. Some have noted that fishers prefer habitats with a high degree of canopy closure (Coulter 1966, Powell 1977, Raphael 1984, Arthur et al. 1989, Thomasma et al. 1991). However, all of the forested habitat types in this study area had a high degree of canopy closure. Fishers did seem to prefer standing trees for dens and resting sites in both seasons but the number of snags at den sites did not appear to be different than the number of snags at random plots.

We also reject the null hypothesis that there are no seasonal differences in forest structure and amounts of woody materials between marten dens and rest sites. Winter resting sites are used primarily for thermal cover. They must provide shelter from precipitation and insulation from cold temperatures. In addition, if the rest site is at or below ground level the animal must have access to these sites through deep snows. It was not surprising that winter rest sites used by martens, which were mostly at or below ground level, had more structure and woody materials in the surrounding areas than spring dens that permitted subnivean access. In spring, when sites changed to standing trees with elevated entrances, the relationship to woody material and forest structure disappeared. For fishers, which showed an apparent preference for standing tree dens with elevated entrances, it was understandable that there was no relationship with CWD.

Martens and fishers use very different rest sites and select sites based on different criteria during the winter. There is no competition for winter thermal rest sites between these two closely related, sympatric carnivores because of the different types of sites used. However, spring den sites are strikingly similar between the two species. We found no difference in any tree characteristic of spring dens. Future research should determine the availability of potential maternal den sites because, if limited, competition for these sites may be occurring.

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CHARACTERISTICS OF RESTING AND DENNING SITES OF AMERICAN MARTENS IN CENTRAL OREGON AND WESTERN WASHINGTON

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Abstract: Resting and denning sites are important habitat components of the American marten (*Martes americana*). Resting sites offer refugia from predation and protection from thermal stress; denning sites have similar functions and also offer such protection for young. Thus, rates of survival and fecundity are likely greater when higher quality denning sites are available. To better understand the attributes of resting and denning sites, we investigated structural characteristics of these sites in relation to forest structure and composition in 2 study areas, a western hemlock (*Tsuga heterophylla*) and Pacific silver fir (*Abies amabilis*) dominated site in the western Cascade Range of Washington and a lodgepole pine (*Pinus contorta*) dominated site in the eastern Cascade Range of central Oregon. We sampled 391 resting and 26 denning sites in Washington and 261 resting and 31 denning sites in Oregon. In Washington, 48% of rest sites were in live trees, 21% in standing dead trees (snags), 9% in downed wood, 13% in logging slash and other human artifacts, and 10% in other ground structures. In Oregon, only 7% of sites were in live trees, 9% were in snags, 22% in downed wood, 45% in logging slash, and 17% in other ground structures. In Washington, 85% of denning sites were in live trees and snags; few sites were in logs or logging residue. In Oregon, 35% of denning sites were in live trees and snags, 32% were in logs, and 29% were in slash. Slash piles were 4 times more abundant in Oregon than in Washington, so selection reflected availability. Martens selected structures from the largest trees available in each study site. Live trees and snags used for resting and denning sites averaged 88 cm dbh in Washington and 57 cm dbh in Oregon. In Washington, 90% of resting and denning sites were in trees >50 cm dbh, which represented 28% of the available trees. In the Oregon study, trees were smaller and 76% of selected sites were in trees >50 cm; only 3% of available trees were that large. Forest operations that result in the removal of large-diameter trees will reduce the number of preferred resting and denning sites. We estimate that retention of about 3 moderately decayed, large-diameter trees, snags or logs per ha will likely meet resting and denning habitat needs of martens and that logging slash, if composed of sufficiently large material, can substitute for some of these sites.

Introduction

American martens (*Martes americana*) are largely restricted to conifer-dominated forests, and have been characterized as among the most habitat-specialized of North American mammals (Buskirk et al. 1987, Buskirk and Powell 1994). However, little is known about which attributes of the conifer forest might be most important in defining quality of marten habitat and thus contributing to fitness of individuals. Comparing patterns of habitat selection in highly contrasting forest environments might lead to insights in identifying key attributes of marten habitat that contribute to meeting life requisites of the species. Martens are highly selective of microenvironments for thermal cover and protection from predators (Buskirk et al. 1989, Buskirk and Ruggiero 1994). Resting sites and denning sites are 2 key microhabitats that contribute to fitness. An animal's choice of resting site influences its vulnerability to predation and protection from inclement weather (Buskirk et al. 1989). In addition, the choice of denning site affects vulnerability of both the female and her offspring (Buskirk and Ruggiero 1994). Therefore, we chose to focus on these 2 habitat features. In this study, we compare attributes of resting sites and maternal dens in 2 contrasting study areas, 1 on the western slopes of the Cascade Range in Washington and 1 on the eastern slope of the Cascade Range in Oregon.

Methods

Study Area

The Washington study area lies mostly on the west slope of the Cascade Range, 39 km northeast of Mount Rainier National Park in the White River Ranger District (US Forest Service). Western hemlock (*Tsuga heterophylla*) and Pacific silver fir (*Abies amabilis*) are the dominant canopy and understory trees, with noble fir (*A. procera*), subalpine fir (*A. lasiocarpa*), Douglas-fir (*Pseudotsuga menziesii*), western red cedar (*Thuja plicata*), and other conifers present. A shrub layer of huckleberries (*Vaccinium* spp.) is typically present. Elevations range from about 760-1830 m. The topography is relatively steep with deeply dissected slopes and many small streams. Although snowfall is high and accounts for most of the precipitation, there is a maritime influence and temperatures are moderate. Mean annual temperature is 5.5°C (mean January minimum is -6.6°C and mean July maximum is 21.1°C). Mean annual precipitation is 2.7 m with 9.8 m snow accumulation (Franklin and Dyrness 1973). Much of the forest is in a mature, old-growth condition, but timber cutting has resulted in a mosaic of cutover and uncut forest. Slash piles are infrequent and occur in clearcut patches with regenerating young conifers.

The Oregon study site is east of the Cascade crest on a high plateau 54 km northeast of Mount Mazama (Crater Lake), in the Chemult Ranger District (US Forest Service). It is a very different environment from the Washington study area. The plateau is about 1675 m in elevation. The pumice soil from the eruption of Mount Mazama helps sustain a climax forest of lodgepole pine (*Pinus contorta*) with a bitterbrush (*Purshia tridentata*) shrub component (Franklin and Dyrness 1973). Small hills and buttes interrupt the otherwise flat topography and are dominated by ponderosa pine *(Pinus ponderosa*) or mixed conifer (*Abies* and *Pinus* spp.). Most streams are very low gradient and form a network of meadows. These streams are usually ephemeral in nature; permanent water is isolated to one stream and artificial sources. Because of the effects of the Cascades rain shadow, air temperature is colder in winter and warmer in summer, with more frequent cloud-free periods than in our Washington study area. Mean annual temperature is 5.3°C (ranging from means of -11.1°C in January to 28.2°C in July). Mean annual precipitation is 0.68 m, with 4.2 m of snow (Franklin and Dyrness 1973). Much of the forest has been harvested but selective cutting and seed-tree retention is typical. Slash piles resulting from timber cutting and road construction are frequent and occur along landings surrounded by forest cover.

Field Techniques

Martens were trapped year-round in single-door wire live traps (Models 202 & 205, Tomahawk Live-trap Co.). A plywood box was attached to the end of each trap to prevent hypothermia and stress. Captured animals were immobilized with ketamine hydrochloride, fitted with radio-collars (various types were used), and given individual tattoos on the upper lip. We attempted to locate martens about twice per week using triangulation following methods described by Guetterman et al. (1991). To locate maternal dens, we usually monitored adult females daily from the time of parturition to kit independence.

We used characteristics of the transmitter signal to determine if a marten was resting. During triangulation, we determined whether the transmitter signal was steady or fluctuating. If the signal was steady for the length of the triangulation or for 10 min, we suspected the animal was resting. When feasible, we determined the exact location of these martens by walking in to the site. If the animal was frightened off at our approach or seemed to be active, the structure was not considered a resting site. However, if the marten was apparently resting, we marked the site with flagging and returned to it at a later date for characterization to minimize disturbance to the animal. Each site was assigned a precision level of 1 (visual or exact location at site known), 2 (specific resting site structure known), or 3 (vicinity known, but not specific structure). Site characterization was usually accomplished within a week of radio-location to ensure that

habitat features had not changed. However, features that might quickly change, such as snow depth, were recorded on the day of the location.

To characterize a site, field crews marked 2 concentric circular plots, measuring 11.3 m and 39.9 m radius and centered on the site. Most vegetative data were recorded in the small plot only, including visual estimates of ground cover, understory and midstory. Standing live trees >10 cm dbh were counted by dbh class (Washington: 10.0-25.0, 25.1-50.0, 50.1-100.0, >100 cm. Oregon: 10.0-25.0, 25.1-50.0, 50.1-75.0, >75 cm). For standing dead trees (snags), we also recorded decay class using the classification of Cline et al. (1980). Snag decay classes represent increasing stages of deterioration from class 1 (recently killed trees that are mostly intact) to class 5 (decayed heartwood and sapwood, broken top, sloughing of all branches and bark). We estimated length of fallen logs within plots and recorded cumulative length by 5 decay classes (Maser et al. 1979) and dbh class. Log decay classes represented increasing degrees of decomposition from decay class 1 (mostly intact logs resting above ground surface) to decay class 5 (advanced decay, mostly submerged in ground). We recorded canopy closure using a convex spherical densiometer in 4 cardinal directions, 5 m from the site's center, and averaged. Counts of larger trees, snags, and fallen logs (in Washington >100 cm dbh; in Oregon >75 cm dbh) were obtained from the larger plot. Additional variables were recorded when we knew the exact location of the animal, including the type of structure, the location of the animal within the structure, and measurements of the structure and entrance. In Oregon, the exact location of the site was determined with a global positioning system (Pathfinder, Trimble Navigation, Sunnyvale, California).

Each site was assigned an individual number reflecting the marten's tattoo number and the sequential (usually) number for the site, and re-uses. The first time any site was used, it was termed an individual site. Subsequent uses by the same marten were considered re-uses. Use of an individual site by a different marten was called a secondary use. All sites were initially considered resting sites, but if it was determined that a female probably had young there as well, it was considered a maternal den site. For our purposes, the term *den* implied a *maternal den*, which included both natal (the site where kits are born) and postnatal (sites used subsequent to birth of kits) structures (Jones et al., this volume). Sites where the female resided apart from the kits during this time were considered resting sites rather than dens. Sites were confirmed if kits were seen or distinctly heard.

A number of criteria were used to designate dens, since kit confirmation was not always possible, particularly in Washington. We compiled information on the reproductive status of female martens trapped between 1 March and 1 October. All but 1 of the martens from Washington that we considered to be denning were known to be pregnant or lactating. We considered nipple enlargement an indicator

of reproductive success. Time of year of occupancy was also a factor. A female that apparently reproduced was likely to be at a den during the appropriate time of year (especially May and June). We also looked at the length of time a female spent at a given site; non-denning animals do not typically re-use sites for long periods. In addition, we considered whether animals used intervening resting sites. Use of such sites early in the season suggested they were not denning. However, martens do change dens.

Data Analysis

To compare frequency of use of structures for resting or denning between study areas, time periods, or sexes, we pooled some of the structures into more general classes. Downed wood included natural logs, stumps, and other coarse woody debris. Slash included piled and scattered logging residue, and other artificially manipulated structures. Ground included rock, ground surface, below-ground burrows, middens, and subnivean sites of unknown structure. We compared characteristics of resting sites for 2 categories of snow cover based on presence of snow on the sample plot; snow was either present or absent. Frequencies were compared using chi-square tests for homogeneity of proportions.

To estimate selectivity of various attributes of resting and denning sites, we compared frequencies of use to availability. Availability was estimated from measurements taken on the habitat plots around each resting or denning site. For this analysis, availability refers to frequency of features at the microsite surrounding used sites (pooled across all sites), not to features at random sites within home ranges or within overall study areas. For estimates of availability of species of live trees and snags, we limited the analysis to stems >50 cm dbh in Washington and >25 cm dbh in Oregon.

We compared spatial distributions of resting and denning sites to the location of streams using a geographic information system (ARC/INFO, Environmental Research Systems Institute, Inc., Redlands, California, USA). For each animal, we plotted the locations of all resting or denning sites onto a base map within a home-range boundary estimated from the minimum convex polygon surrounding all locations for that animal. We obtained hydrologic information from each forest and plotted all permanent and intermittent streams within each home range. We then computed the shortest distance from each resting or denning site to its nearest stream and computed mean site-to-stream distance for each animal. For comparison we defined 25 randomly located points within each home range and computed distance to stream in the same way. We then used paired *t*-tests to compare mean distances to streams for used versus random points within home ranges.

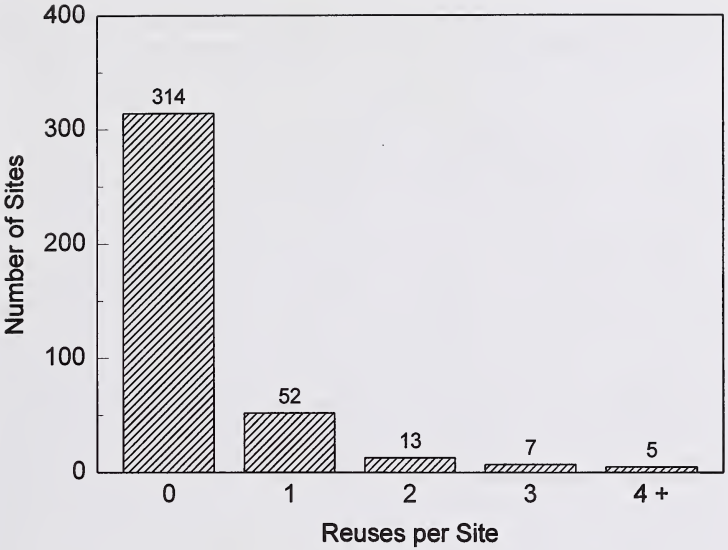

Figure 1. Frequency distribution of number of repeated uses of individual resting sites by American martens in the Cascade Range, Washington.

Results

Resting Sites

We located a total of 652 individual resting sites; 391 used by 23 martens in Washington and 261 sites used by 46 martens in Oregon. About 20% of all resting sites were used more than once in each of the Washington (Fig. 1) and Oregon study areas. In 1 case, we documented 12 uses of the same site. We recognized 14 different types of structure (Table 1); we were not able to identify the exact location in 14 cases and these unknowns were excluded from subsequent analyses. Frequency of use of resting sites differed between Washington and Oregon ($\chi^2 = 179.1$, df = 4, $P < 0.001$). Martens in Washington most often selected live trees and snags whereas martens in Oregon selected logging slash and logs. Slash piles were about 4 times more abundant in Oregon than in Washington, and the more frequent use of slash in Oregon probably reflected its greater availability there. However, it is possible that martens in Oregon were more easily disturbed in non-slash structures, which could cause undersampling of such sites. Resting site selection did not differ between males and females in

Table 1. Structures used as resting sites by American martens in the Cascade Ranges of Washington and Oregon (percentage in parentheses).

	Washington		Oregon	
Structure	Resting	Denning	Resting	Denning
Live tree	181 (46)	14 (54)	18 (7)	6 (19)
Snag	81 (21)	8 (31)	24 (9)	5 (16)
Windthrown logs	17 (4)	0	6 (2)	0
Single log - bole	7 (2)	1 (4)	48 (18)	10 (32)
Single log - root	9 (2)	0	2 (1)	0
Cut stump	3 (1)	0	1 (<1)	0
Logging slash	34 (9)	2 (8)	113 (43)	9 (29)
Roadside debris[a]	11 (3)	0	1 (<1)	0
Rock	14 (4)	1 (4)	2 (1)	0
Ground	9 (2)	0	1 (<1)	0
Subnivean[b]	12 (3)	0	39 (15)	0
Animal burrow	1 (<1)	0	1 (<1)	1 (3)
Squirrel midden	1 (<1)	0	0	0
Cabin	0	0	2 (1)	0
Unknown	11 (3)	0	3 (1)	0
Total	391	26	261	31

[a] Includes rock, soil, and wood debris from road or landing construction.

[b] Includes only those sites where structure being used was unknown.

Washington ($\chi^2 = 5.0$, df = 4, $P = 0.286$; Table 2) or in Oregon ($\chi^2 = 1.7$, df = 4, $P = 0.777$; Table 3).

Selection of resting sites differed between snow and snow-free periods in Washington ($\chi^2 = 13.7$, df = 4, $P = 0.008$) and Oregon ($\chi^2 = 83.8$, df = 4, $P < 0.001$). In Washington, for example, 17% of resting sites were in slash when snow was absent but only 5% were in slash when snow was present (Table 2). Seasonal differences were greater in Oregon; 60% of resting sites were in slash in snow-free times and 17% were in slash in times of snow. In winter, martens in Oregon frequently used coarse woody debris and ground sites (including

Table 2. Types of resting sites used by male and female American martens during snow and snow-free periods in the Cascade Range, Washington, 1989-1994 (percentages in parentheses).

	Snow		Snow-free		
Structure	Male	Female	Male	Female	Total
Live tree	49 (50)	24 (57)	59 (41)	49 (52)	181 (48)
Snag	19 (19)	9 (21)	31 (21)	22 (23)	81 (21)
Downed wood[a]	11 (11)	4 (10)	13 (9)	5 (5)	33 (9)
Slash[b]	6 (6)	1 (2)	28 (19)	13 (14)	48 (13)
Ground[c]	13 (13)	4 (10)	14 (10)	6 (6)	37 (10)
Total	98	42	145	95	380

[a] Includes natural logs, stumps, and other coarse woody debris.

[b] Logging slash and other artificial structures.

[c] Includes rock, ground surface, below-ground burrows, middens, and subnivean sites of unknown structure.

subnivean, Table 3). In Oregon, 76% of 97 resting sites were in subnivean locations, whereas 22% of 146 resting sites in Washington were subnivean.

Martens tended to select sites with greater canopy closure during snow periods than during snow-free periods. In Washington, mean canopy closure at resting sites was 76% in snow periods and 67% in snow-free periods ($t = 2.54$, $P = 0.011$). In Oregon, mean canopy closure at resting sites was 36% in snow periods and 27% in snow-free periods ($t = 3.13$, $P = 0.002$).

In Washington, martens rested in 9 different species of conifer; 83% of resting sites were in 4 of these species and nearly half were in western hemlock (Fig. 2). Although frequency of use differed from availability ($\chi^2 = 60.2$, df = 4, $P < 0.001$), proportions of use were in the same rank order as availability. In Oregon, martens used 4 species of conifer, none of which were the species used in Washington, reflecting the different composition of the study areas. Use differed from availability ($\chi^2 = 34.3$, df = 3, $P < 0.001$), with ponderosa pine being used more frequently than expected and lodgepole pine less frequently (Fig. 2).

Martens selected more of the larger diameter trees and snags for resting than indicated by availability in both study areas (Fig. 3). In Washington, trees and snags >50 cm dbh were used with greater-than-expected frequency, whereas trees <50 cm dbh were used less frequently than expected ($\chi^2 = 1936$, df = 3, $P < 0.001$). Mean diameter (± SE) of live trees used for resting was 90 ± 6.7 cm dbh; mean diameter of snags was 82 ± 9.2 cm. In Oregon, pattern of selection

Table 3. Types of resting sites used by male and female American martens during snow and snow-free periods in the Cascade Range, Oregon, 1993-1995 (percentages in parentheses).

	Snow		Snow-free		
Structure	Male	Female	Male	Female	Total
Live tree	3 (6)	1 (2)	8 (8)	6 (11)	18 (7)
Snag	4 (8)	2 (5)	12 (11)	6 (11)	24 (9)
Downed wood[a]	17 (33)	13 (30)	15 (14)	11 (19)	56 (22)
Slash[b]	7 (13)	9 (21)	67 (63)	32 (56)	115 (45)
Ground[c]	21 (40)	18 (42)	4 (4)	2 (4)	45 (17)
Total	52	43	106	57	258

[a] Includes natural logs, stumps, and other coarse woody debris.

[b] Logging slash and other artificial structures.

[c] Includes rock, ground surface, below-ground burrows, middens, and subnivean sites of unknown structure.

was similar to that in Washington, with trees and snags >50 cm used more frequently than expected ($\chi^2 = 446$, df = 3, $P < 0.001$). Mean diameter of live trees used for resting was 47 ± 11.0 cm and mean diameter of snags was 66 ± 13.7 cm.

Martens used snags and logs in all decay classes, but used moderately decayed structures most frequently (Fig. 4). In Washington, frequency of use exceeded availability of decay class 4 snags; decay class 3 snags were used less frequently than availability ($\chi^2 = 29.9$, df = 4, $P < 0.001$). Sample sizes from Oregon were not large enough for statistical analysis, but snags in decay classes 1 through 4 were used with nearly equal frequency (5 to 6 sites each) and we found only 2 rest sites in decay class 5 snags. In Oregon, 29 of 41 resting sites in logs were in decay classes 2 and 3; 5 and 6 sites were in decay classes 1 and 4, respectively. Only 1 rest site was in a class 5 log. We found only 5 rest sites in logs in Washington; 3 were in decay class 3 and 2 in decay class 4 logs.

The distribution of resting sites was strongly tied to streams in Washington (Fig. 5). Streams were frequent in home ranges of martens in the Washington study area, and resting sites tended to be located near streams. Mean distance to streams of resting sites in 11 home ranges (59 ± 5.2 m) was significantly less ($t = 4.0$, df = 10, $P = 0.003$) than mean distance from random points to streams within the same home ranges (85 ± 6.9 m). In contrast, streams were infrequent in the Oregon study area, and we observed weaker evidence that martens selectively located resting sites near streams in that study area (Fig. 6). In Oregon,

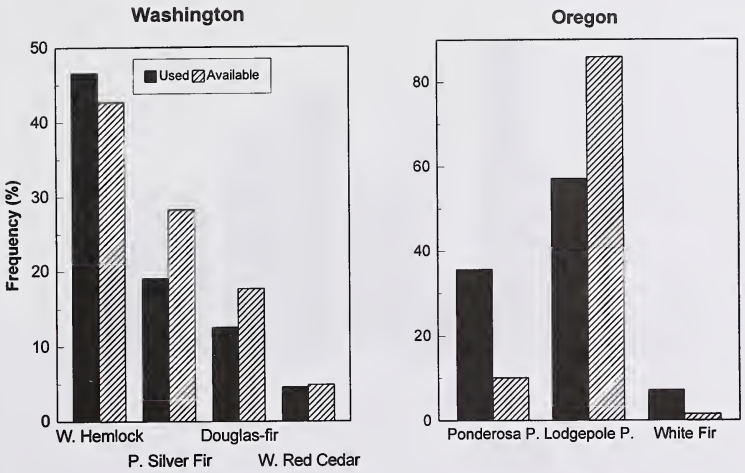

Figure 2. Frequency of use and availability of species of live trees and snags used as resting sites by American martens in the Cascade Ranges of Washington (n = 262) and Oregon (n = 42).

resting sites within 12 home ranges averaged 546 ± 101 m from streams and randomly located points within the same home ranges averaged 599 ± 67 m from streams (t = 0.8, df = 11, P = 0.468).

Denning Sites

We found 57 denning sites, 26 in the Washington study area and 31 in Oregon (Table 1). Selection of structures differed between the two study areas (χ^2 = 15.4, df = 4, P = 0.004). As with selection of resting sites, female martens denned more often in coarse woody debris and slash in Oregon than in Washington and denned more often in live trees and snags in Washington. Canopy closure at denning sites was 77% in Washington and 30% in Oregon and did not differ from that of resting sites in either study site (t = 1.0, P = 0.316 in Washington; t = 0.1, P = 0.939 in Oregon). Martens denned in different species in Washington than in Oregon, reflecting the differences in tree species between study areas. In Washington, of 22 dens in live trees and snags, 13 were in western hemlock, 5 were in Pacific silver fir, 2 were in Douglas-fir, 1 was in an Alaska-cedar (*Chamaecyparis nootkatensis*), and 1 was in an unknown species. In Oregon, 8 of 11 dens in live trees and snags were in ponderosa pine and 3 were in lodgepole pine.

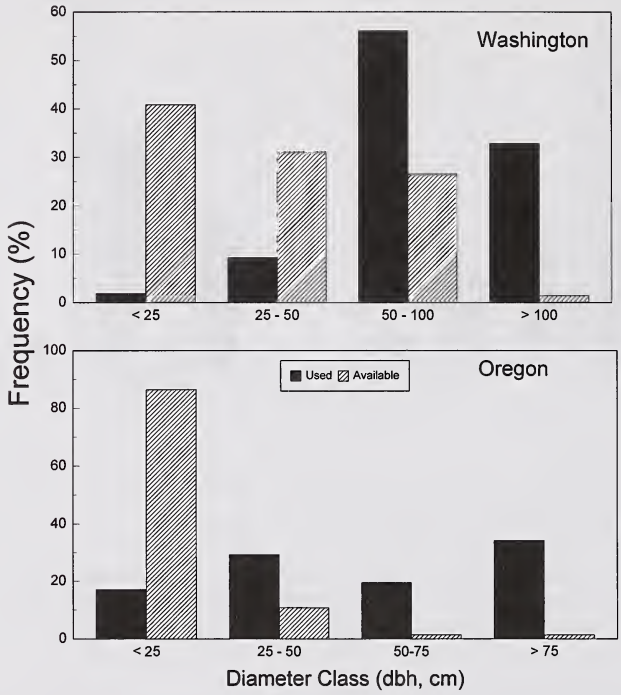

Figure 3. Frequency of use and availability of diameter classes (dbh) of live trees and snags used as resting sites by American martens in the Cascade Ranges of Washington (n = 262) and Oregon (n = 41).

In Washington, martens denned in structures similar to resting sites, but there was a greater use of above-ground structures for dens (85%) than for resting sites (69%). In Oregon, this pattern was more pronounced. The use of above-ground structures for denning (35%) was twice that for resting (16%). However, logs were used more for denning (32%) than for resting (18%) sites. In Oregon, slash piles were used less frequently for dens (30%) than for resting sites (43%). Slash was used primarily for post-natal denning (7 of 10 dens in slash).

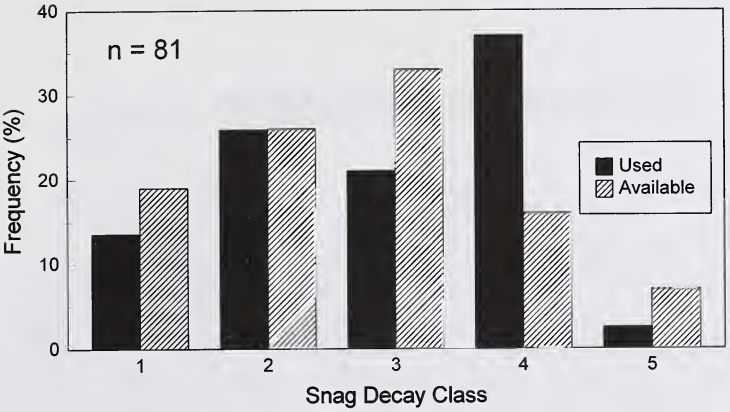

Figure 4. Frequency of use and availability of decay classes (Cline et al. 1980) of snags used as resting sites by American martens in the Cascade Range, Washington. Decay classes 1 to 5 represent increasing stages of decomposition.

Although larger, diameters of live trees and snags used as dens (98 ± 7.0 cm dbh) did not differ significantly from those used as resting sites in Washington (88 ± 2.0 cm; $t = 1.34$, $P = 0.180$). In Oregon, denning sites (81 ± 8.1 cm dbh) were significantly larger than resting sites (57 ± 4.9 cm dbh; $t = 2.3$, $P = 0.026$). Mean height of marten dens was 25.0 m (range 0 - 48.3 m) in Washington and 18.9 m (range 0 - 32.3 m) in Oregon. Martens denned in logs and snags of decay classes 1 to 4 in Washington and decay classes 1 to 3 in Oregon (Fig. 7).

Discussion

Our 2 study areas differed in the structure and composition of overstory cover and in characteristics of understory structures. They involved completely different species of trees, canopy closure, patterns of logging, topography, and streams. Variation in patterns of resting and denning site selection between the 2 study areas reflected differences in structure and composition of these areas. Similarly, Brainerd et al. (1995), working in Norway and Sweden, noted differences in resting site use by the Eurasian pine marten (*Martes martes*) compared with resting sites from the Finland and Russia study areas of Pulliainen (1981). Our observations support Buskirk and Powell's (1994) conclusion that physical structure of a stand seems to be more important than species composition. The 2

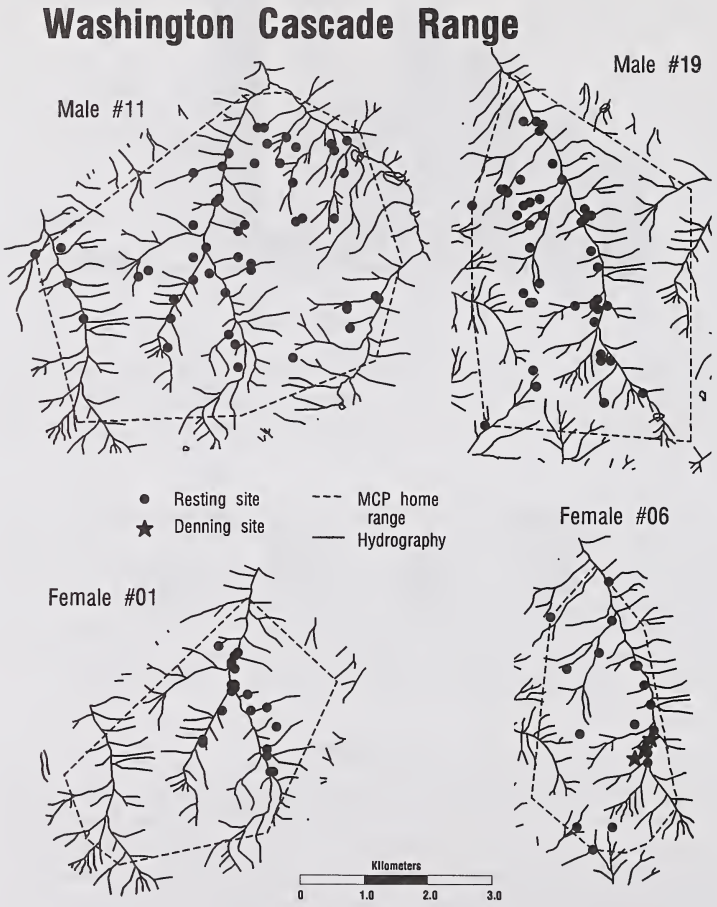

Figure 5. Distribution of resting sites and maternal dens for a sample of 2 male and 2 female American martens in relation to permanent and intermittent streams within minimum convex polygon (MCP) home ranges, Cascade Range, Washington.

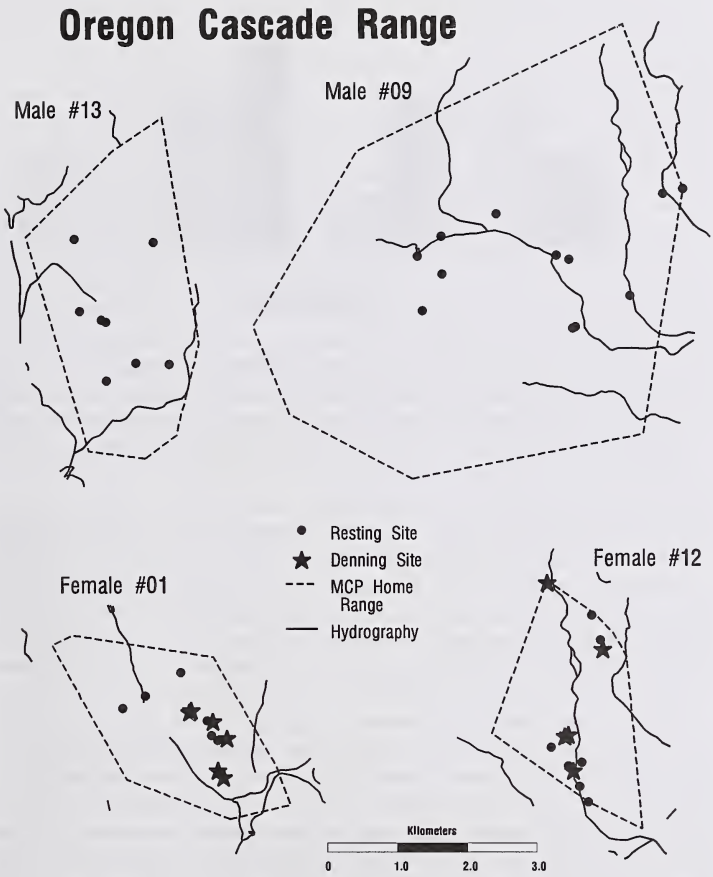

Figure 6. Distribution of resting sites and maternal dens for a sample of 2 male and 2 female American martens in relation to permanent and intermittent streams within minimum convex polygon (MCP) home ranges, Cascade Range, Oregon.

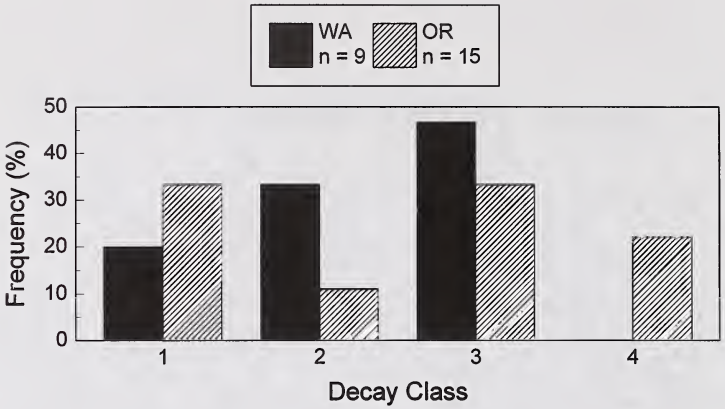

Figure 7. Frequency of use of decay classes of snags (Cline et al. 1980) and logs (Maser et al. 1979) used as maternal dens by American martens in the Cascade Ranges of Washington and Oregon. Decay classes 1 to 4 represent increasing stages of decomposition. No dens were found in class 5 snags or logs in either study area.

study areas had no common tree species and martens used completely different species for resting and denning. However, in both areas, they selected large-diameter trees, logs, and snags and used snags and logs of intermediate levels of decay. Although martens are sexually dimorphic, with adult males having 50-60% greater body mass than adult females (Nagorsen 1994), we found no evidence of differences in attributes of resting sites selected by male and female martens.

We found strong seasonal differences on selection of resting sites in both study areas. Many studies have shown shifts in use of different structures between summer and winter. In summer, martens often rest in sites above the ground, usually in the canopy layer (Simon 1980, Burnett 1981, Buskirk et al. 1987, Martin and Barrett 1991). In winter, or during periods of snow cover, resting sites are often in snags and logs below the snow surface (Steventon and Major 1982, Spencer 1987, Martin and Barrett 1991). Buskirk et al. (1989) found that martens used subnivean sites associated with coarse woody debris during the coldest weather and that they used above snow sites in warmer weather. Some of our results were consistent with these general observations. In our Oregon study area, martens used downed wood and ground sites much more frequently during snow periods than during snow-free periods. However, our observations of

greater use of slash piles during snow-free periods than during snow periods in both study areas does not fit the general observation of greater use of downed wood near the ground during snow periods. We suspect this difference reflects the thermoregulatory properties of slash piles, which may not offer the advantages of larger logs or other subnivean sites. Martens used stands with greater canopy closure during snow periods than during snow-free periods, in both of our study areas, but this difference may not be independent of slash use. Slash piles occur in landings that have low overhead canopy cover. Other studies have also shown that martens use stands that are more mature and have greater canopy closure in winter than in summer (Campbell 1979, Soutiere 1979, Steventon and Major 1982, Wilbert 1992, Buskirk and Powell 1994, Buskirk and Ruggiero 1994), perhaps because of thermal advantages and protection from predators (Buskirk et al. 1989). Therefore, martens may be less likely to use slash piles in winter because piles occur in less favorable habitats or perhaps because the piles themselves offer lower thermoregulatory advantage. Conversely, differences in canopy closure at sites used in winter versus summer may reflect seasonal differences in selection of particular structures. In our Washington site, martens used live trees and snags throughout the year; they rarely used subnivean sites for resting. This behavior may reflect favorable thermal conditions in an area with a moderate temperature regime.

Although our sample of dens was considerably smaller than that of resting sites, there were some apparent differences. For denning females in Oregon, there was a shift to above-ground structures (trees and snags). Brainerd et al. (1995) also reported this vertical shift for the Eurasian pine marten in Scandinavia. They suggested the shift from near-ground resting sites to above-ground denning sites was largely a response of pine martens to predators (particularly red fox, *Vulpes vulpes*). Kits would be better protected in internal, arboreal dens than ground-level or external, arboreal nests. This protection would seem a logical explanation for the American marten at the Oregon site as well, but the substantial use of logs as dens is contradictory. However, because the diameter of log dens tends to be large and the interior is protected by stobs and side chambers (Jones et al., this volume), protection of kits from ground predators (especially prior to weaning) would be afforded. Large-diameter structures, be they near-ground or arboreal, also provide the greater space demands for a family of martens (Brainerd et al. 1995)

The differences between denning and resting sites were not as pronounced in Washington. Large, live trees and snags, particularly western hemlock, served to provide shelter for both functions. Near ground-level sites received little use in Washington. This observation suggests that old canopy trees and snags usually provided the requisites for both resting and denning. Clearly, there is a need to

increase our sample of dens and to explore the differences of resting and denning structures in different physiographic regions.

The apparent importance of habitats near streams differed between our 2 study areas (Figs. 5, 6). Several authors have reported selection of riparian zones by martens for resting (Buskirk et al. 1989) or foraging (Spencer et al. 1983, Spencer and Zielinski 1983). We believe that our evidence of strong selection of sites near streams for resting in Washington reflects the presence of better habitat there. In that study area, the steeply dissected slopes cause large logs to accumulate nearer the bottoms of the slopes along streams. In addition, past cutting practices have favored retention of larger trees along streamsides. It is also likely that the more mesic conditions along slope bottoms create more favorable microclimates and greater understory development along stream than on upland sites, although we have no supporting data. Fallen logs along streams may also support subnivean access sites (Corn and Raphael 1992) and good hunting opportunities. Buskirk et al. (1989) also believed that streamside locations were more likely to support favorable microhabitats and structures for resting. We found less evidence of selection of streamside habitats by martens on our Oregon study area. In that area, the flat topography did not create a contrast between streamside and upland habitats such as we observed in Washington. Instead, we found the opposite: upland sites were more likely to support large-diameter ponderosa pines that were frequently used as resting and denning sites. The comparison of conditions at the 2 study areas leads to a conclusion that it is the structural attributes of a site that determine its suitability for resting or denning, not its proximity to water. In Washington, the better sites occur near water and we observed a close relationship between streams and locations of resting sites. In Oregon we saw a weaker relationship between streams and resting sites.

Management Implications

We draw 2 important conclusions from this study. First, it is large diameter that seems to be the critical feature of potential resting and denning sites. In both study areas, trees, snags and logs with diameters of 50 cm dbh or larger were selected at rates significantly greater than predicted from availability. Second, when natural sites were scarce, martens used artificial structures such as slash piles as long as the size of the individual pieces and total volume of material met some minimum criteria. However, our data showed a strong shift away from slash use during winter, so management should not be based solely on slash retention. Using this information, it is possible to speculate on the density of structures that must be available to support martens.

If each marten uses 1 resting site or den per day, it would need 365 sites per year. Assuming an average lifespan of 5 years (Strickland and Douglas 1987) and a factor of 0.68 for re-use (Fig. 1), an animal might use 1241 sites during its lifetime.

Based on estimated average home ranges (minimum convex polygon) of 1780 ha for male martens and 580 ha for females (Raphael and Jones, unpublished data), we estimate total density (sites per ha) of these structures of 0.70 for males and 2.14 for females, with a grand total of 2.84 sites/ha. From proportions of sites in each structure (Table 2), we estimate a pair of martens might use 1.4 live trees, 0.6 snags, 0.2 logs, and 0.4 slash piles per ha in Washington. For Oregon, we estimate a pair of martens might use 0.2 live trees, 0.3 snags, 0.6 logs, and 1.3 slash piles per ha (Table 3). In each case, these sites should meet the appropriate size and decay criteria.

These estimates imply that requirements for numbers of resting and denning structures are rather modest and should be relatively easy to accommodate in managed forests. The extent to which artificial structures can substitute for natural structures is unknown, but our comparison of the 2 study areas suggests that such substitution may be possible if the structures can be rendered useable during winter.

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SEASONAL SELECTION OF HABITATS BY RESTING MARTENS IN MAINE

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Abstract: American martens (*Martes americana*) use a variety of resting sites between foraging episodes, and the vertical position of resting sites may vary by season. Martens tend to rest above the ground during summer, and almost exclusively beneath the snow surface during winter. Few studies have evaluated whether martens are selective in choice of resting habitats based on the amount of forest structure, or whether they are opportunistic in resting-site choice. We described and compared with availability the seasonal characteristics of marten resting sites, tested for seasonal selection of forest overstory types by resting martens, and compared measures of forest understory and ground structure among forest overstory types in a second-growth forest in Maine dominated by deciduous and deciduous-coniferous mixed forest types. During summer, martens tended to rest in trees or snags, whereas during winter, they usually rested in subnivean sites ($P < 0.001$). The distribution of resting sites among forest overstory types did not differ from availability during summer ($P = 0.164$) or winter ($P = 0.510$), despite the fact that coniferous stands had significantly ($P \leq 0.007$)

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more logs on the forest floor and standing snags than did both mixed and deciduous stands. Forest overstory, understory, and ground structure had little effect on the selection of resting sites during summer or winter, based on multivariate logistic regression models. We conclude that forest structure occurred above thresholds at which resting sites limit use of habitat by martens. We recommend further study to document thresholds of forest structure required by martens, and to examine the influence of timber harvesting activities on long-term forest structure.

Introduction

Structural characteristics of habitats used for resting by the American marten (*Martes americana*) have been studied throughout the western portion of the species' range (e.g., Buskirk 1984, Spencer 1987, Buskirk et al. 1989, Martin and Barrett 1991, Corn and Raphael 1992). Resting sites are generally associated with forest attributes that provide vertical or horizontal structure, such as trees, snags, downed logs, stumps, root masses, rock crevices, and squirrel (*Tamiasciurus* spp.) middens (Strickland et al. 1982). Selection of resting sites is thought to be based on thermal properties, protection from predators, and proximity to, and accessibility of, prey (Buskirk and Powell 1994).

Several studies have reported seasonal variation in the vertical position of resting sites (Steventon and Major 1982, Buskirk 1984, Spencer 1987, Martin and Barrett 1991, Wilbert 1992). During winter, when energetic constraints are severe (Buskirk et al. 1988), martens tend to rest in subnivean spaces, which can have a higher ambient temperature than above the snow surface (Taylor 1993). Subnivean spaces are accessed through breaks in the snow cover created by angled logs, large tree boles, low branches, stumps, snags, root masses, rock outcrops, or, less commonly, by burrowing through the snow cover (Corn and Raphael 1992). Subnivean spaces surrounded by partially decomposed coarse woody debris probably provide martens with a thermally neutral resting environment (Buskirk et al. 1989), and may provide access to potential prey that also focus activity below the snow surface (Sherburne and Bissonette 1993).

During summer, martens tend to rest in tree crowns or snags, where ambient temperature may be lower than at the ground surface (Smith 1990). Resting sites in trees may occur in "witches' brooms" (dense growths of branches caused by insects or epiphytes), cavities, or in the forks of limbs (Wynne and Sherburne 1984, Spencer 1987). In the western United States, snags are often used by martens for resting during summer (Campbell 1979, Spencer 1987, Martin and Barrett 1991); however, limited information from studies in eastern North America has included no observations of martens using snags during summer (Mech and Rogers 1977, Masters 1980, Steventon and Major 1982).

Some studies have reported that martens rest in certain forest overstory types disproportionately to their availability (Spencer 1987, Buskirk et al. 1989).

Selection by resting martens for forest overstory species composition has been attributed to differences in the amount of ground structure in different forest types (Buskirk et al. 1989). Such a relationship assumes that the availability of resting sites limits habitat use, and that a relationship exists between ground structure and overstory species composition. Alternatively, if resting sites are not a limiting factor, then habitat use may be dictated by a habitat component other than abundance of resting sites. Use of resting sites may be based on the relative availability of potential resting sites (Martin and Barrett 1983) in an area being occupied by a marten for other reasons. For example, Thompson and Colgan (1994) documented that, despite greater access to subnivean spaces in unlogged areas vs. logged areas, martens hunted beneath the snow at the same rate in both areas. Thus, availability of potential resting sites may not be limiting to the marten throughout its geographic range (Thompson and Colgan 1994).

The most consistent pattern in resting-site selection by martens is their tendency to use subnivean resting sites in winter and above-ground resting sites in summer. However, much variation in specific structures used for resting sites has been documented (Strickland et al. 1982). Such variation may be related to differences in geology, topology, climate, and the structural characteristics of forests throughout the species' geographic range (Thompson 1991).

Because the seasonal characteristics of resting sites have not been described throughout the range of forest types occupied by the marten, and selection of forest types for resting has not been evaluated relative to measured differences in ground structure, we investigated resting-site selection by martens in an untrapped, unlogged forest in Maine dominated by deciduous and deciduous-coniferous mixed forest types. Our objectives were to describe and compare with availability the seasonal characteristics of marten resting sites, to test for seasonal selection of forest overstory types by resting martens, and to compare measures of forest understory and ground structure among forest overstory types.

Study Area

The study area was located in Piscataquis County, Maine, in the west-central portion of Baxter State Park. The study area was approximately 55 km^2, with elevations from 330 to 735 m. Mean maximum July temperature for the region was 25°C, with mean minimum January temperature of -17°C (McMahon 1990). Average annual snowfall for the region was 3 m, the highest in Maine (McMahon 1990). Most of Baxter State Park has been managed as a wilderness preserve without trapping or timber harvesting since approximately 1960. Prior to legal protection, large-diameter spruce (*Picea* spp.) and white pines (*Pinus strobus*) were selectively harvested from the study area resulting in a mosaic of naturally

disturbed stands, resulting from spruce-budworm (*Choristoneura fumiferana*) mortality, and mature stands dominated by deciduous and mixed deciduous-coniferous forest types. A spruce-budworm epidemic from 1974 to 1984 (Irland et al. 1988) caused mortality of coniferous trees, especially balsam fir (*Abies balsamea*), resulting in stands with reduced canopy closure and apparent increases in amounts of ground structure in the form of snags, stumps, root masses, and logs.

Coniferous stands were dominated by balsam fir and red spruce (*Picea rubens*), and included white pine, eastern hemlock (*Tsuga canadensis*), black spruce (*Picea mariana*), northern white cedar (*Thuja occidentalis*), and larch (*Larix laricina*). Deciduous stands included sugar maple (*Acer saccharum*), red maple (*A. rubrum*), yellow birch (*Betula allegheniensis*), paper birch (*B. papyrifera*), big-tooth aspen (*Populus grandidentata*), and American beech (*Fagus grandifolia*). The understory in stands regenerating from extensive spruce-budworm mortality was dominated by balsam fir, maples (*Acer saccharum*, *A. rubrum*, and *A. pensylvanicum*), birches (*Betula* spp.), American mountain-ash (*Sorbus americana*), and raspberry (*Rubus* spp.), depending on site conditions.

Methods

Data Collection

Martens were live-trapped, radio-collared, and radio-tracked from October 1990 to April 1994, using a protocol similar to that described in Katnik et al. (1994). Martens were located every 12-36 hours from 1 May to 30 November and at 10-day intervals from 1 December to 31 March, using ground-based radiotelemetry. We located inactive radio-collared martens by triangulation, using 2 bearings obtained by a single observer at surveyed receiving stations on roads (Phillips 1994). Martens were determined to be resting if telemetry signals were constant for 60 seconds. We located resting martens by homing in on telemetry signals on foot. If signals indicated that the marten became active during our "walk in," we abandoned the search. We obtained resting-site data opportunistically, thus the distribution of our observations may have been influenced by the distance of a marten from the nearest road and by the duration of remaining daylight.

We considered the resting site as the source of the telemetry signal, or the location from which the marten emerged if disturbed. The observer categorized each resting site as being in a tree, snag, stump, log, root mass, rock crevice, or other location (i.e., could not identify a particular structure associated with the signal source). The species composition of the forest overstory in the immediate vicinity of the resting site was visually estimated to be deciduous (<25%

coniferous), mixed (25-75% coniferous), or coniferous (>75% coniferous). Canopy height was visually estimated into 1 of 4 categories: 0-6 m, 6-12 m, 12-18 m, or >18 m. Overhead cover was estimated using a spherical densiometer (Lemmon 1956).

We measured characteristics of understory and ground structure using a pair of 2 × 10-m transects, 1 at an azimuth of 0°, and 1 at an azimuth of 180°, originating from the resting site. Along each transect, observers counted the number of horizontal logs >7.6 cm in diameter that occurred in the 2-m wide transect. Logs were categorized as either <1 m or >1 m in height, based on their estimated average height within the transect. Stumps (<1 m in height) and snags (>1 m in height) were also counted in each transect.

Understory density was measured using a foliage density pole (Griffith and Youtie 1988) at the distal end of each transect. The number of 0.1-m bands in each 0.5-m section of the pole that were >25% obstructed by vegetation, when viewed from the resting site, were counted. Understory density was also measured by counting the number of stems of deciduous and coniferous woody plants <7.6 cm in diameter in each 2 × 10-m transect.

We also measured characteristics of the forest overstory, understory, and ground structure at random sites in the study area, during both summer and winter. Because 75% of all resting sites that we visited occurred <390 m from roads, we sampled only random sites that occurred within 390 m of roads. We navigated to preselected random sites along a bearing from known locations using a compass and pacing to estimate distance. At each random site, overhead cover, canopy height, forest type, foliage density, numbers of deciduous and coniferous stems, and numbers of logs, snags, and stumps were measured using the same protocol used at known resting sites.

Statistical Analysis

We used a G test (Zar 1984) to examine differences in the distribution of resting sites relative to random sites, during both summer and winter, in 3 forest types based on overstory composition: deciduous (<25% coniferous), mixed (25-75% coniferous), and coniferous (>75% coniferous). We used a Fisher exact test (Zar 1984) to examine differences in vertical location of resting sites between summer (1 May to 31 October) and winter (1 December to 31 March). Because of the documented seasonal shift in resting-site location (Steventon and Major 1982, Buskirk 1984, Spencer 1987, Martin and Barrett 1991, Wilbert 1992), we used a one-tailed test of the hypothesis that the proportion of resting sites in trees or snags vs. below the ground or snow was greater during summer than during winter. We used data from random sites in summer to test for differences in measures of ground structure among the 3 forest types, deciduous, mixed, and coniferous, using a Kruskal-Wallis test (Conover 1980). Multiple

comparisons were used to determine which forest types differed, with a pairwise rejection level of 0.017 (i.e., 0.05/3 comparisons), for each Kruskal-Wallis test (one for each measurement).

We used stepwise multiple logistic regression (Hosmer and Lemeshow 1989), with the program LOGIT (Steinberg and Colla 1991), to determine which measurements of forest overstory, understory, and ground structure differed between resting sites and random sites and between resting sites used by males and females. Variables considered for inclusion in models were: overhead cover, canopy height, forest type, foliage density <0.5 m, foliage density 0.5-2.0 m, number of coniferous stems, number of deciduous stems, number of logs <1 m in height, number of logs >1 m in height, number of snags, and number of stumps. Four different models were evaluated: male vs. female resting sites (summer), male vs. female resting sites (winter), resting sites vs. random sites (summer), and resting sites vs. random sites (winter). Summer was defined as 1 May to 31 October (leaf-on) and winter was defined as 1 December to 31 March (leaf-off and generally snow-covered). We excluded April and November because of transitional weather conditions during those months. Only variables that had univariate (Mann-Whitney tests) P-values < 0.10 for tests between cases of the binary response variable were included in the multivariate model (Capen et al. 1986, Schamberger and O'Neil 1986); however, because of their perceived importance in the habitat associations of the marten (e.g., Buskirk and Powell 1994), the variables overhead cover, canopy height, and forest type were included in model development regardless of their univariate differences (Capen et al. 1986).

In the logistic regression, forest type and canopy height were considered categorical variables and were recoded as dummy variables using deviation-from-means cell coding (Hosmer and Lemeshow 1989). We used a mixed stepping procedure for variable reduction among variables chosen for model development (Steinberg and Colla 1991). We used an alpha to remove variables = 0.10 and an alpha to add variables = 0.05 based on recommendations from Steinberg and Colla (1991). The stepwise procedure stopped when all variables in the model were too significant to be removed, and additional variables were not significant enough for addition.

We evaluated the fit of each model using McFadden's rho-squared statistic (Hensher and Johnson 1981) and a jackknife procedure (Efron 1982). McFadden's rho-squared is analogous to a linear regression's r-squared, but with values between 0.2 and 0.4 representing a good model fit (Hensher and Johnson 1981). Using a jackknife approach for each model, we determined the probability of response for each case using equation coefficients obtained from a model excluding that case. We classified probabilities >0.5 as response and <0.5 as no

response. We also examined the mean and standard deviation of the probability of response among both cases of the response variable.

Results

From 1991 to 1994, we visited 73 resting sites of 28 martens during summer (1 May to 31 October) and 67 resting sites of 36 martens during winter (1 December to 31 March). We collected data at 51 random sites in January 1992 and 150 random sites in July 1994. The proportion of resting sites that occurred in trees or snags *versus* below the ground or snow was greater ($P < 0.001$) during summer (68% of 73 resting sites) than during winter (7% of 67 resting sites, Table 1). The distribution of resting sites in deciduous, coniferous, and mixed forest types did not differ from that of random sites during summer ($G = 3.614$, $P = 0.164$) or during winter ($G = 1.347$, $P = 0.510$).

The 3 forest overstory types (deciduous, coniferous, and mixed) differed in most measures of ground structure at summer random sites ($n = 150$) in our study

Table 1. Resting sites used by martens during summer (1 May to 31 October) and winter (1 December to 31 March) in north-central Maine, 1991-1994.

	Summer		Winter	
Site type	*n*	%	*n*	%
Live Trees				
Birch (*Betula* spp.)	3	4.1	1	1.5
Maple (*Acer* spp.)	6	8.2	0	0.0
Spruce (*Picea* spp.)	19	26.0	1	1.5
Fir (*Abies balsamea*)	4	5.5	1	1.5
Cedar (*Thuja occidentalis*)	6	8.2	0	0.0
Other	1	1.4	1	1.5
Snag	11	15.1	1	1.5
Stump	2	2.7	12	17.9
Log	8	11.0	7	10.4
Root mass	4	5.5	12	17.9
Rock crevice	7	9.6	4	6.0
Other[a]	2	2.7	27	40.3
Total	73	100.0	67	100.0

[a] Resting sites that were subterranean or subnivean and could not be associated with a specific structure.

site. The following measurements of ground structure differed by forest type: numbers of deciduous stems ($P < 0.001$), coniferous stems ($P < 0.001$), logs <1 m ($P < 0.001$), logs >1 m ($P = 0.007$), and snags ($P < 0.001$). The number of stumps did not differ ($P = 0.228$) by forest type. Deciduous stands contained fewer coniferous stems, logs <1 m, logs >1 m, and snags than both mixed and coniferous stands. Mixed stands contained fewer logs <1 m and snags than coniferous stands.

During summer, among univariate tests for sex-specific differences in understory and ground structure characteristics, only the number of logs >1 m in height differed ($P < 0.10$) between resting sites used by males ($n = 21$) and females ($n = 49$). A stepwise logistic regression model including the variables forest type, canopy height, overhead cover, and the number of logs >1 m failed to incorporate any significant effects. Thus, we had insufficient evidence to conclude significant effects of measures of forest overstory, understory, or ground structure on sex-specific patterns of resting-site use during summer. During winter, only foliage density <0.5 m differed between the sexes (41 male and 23 female resting sites), and was included in a model with forest type, overhead cover, and canopy height. The stepwise procedure resulted in a significant model ($P = 0.034$) with foliage density <0.5 m as the only significant effect ($P = 0.045$, Table 2); however, the model fit was poor (McFadden's rho-squared = 0.054). The jackknife procedure correctly classified 80% of male, 0% of female, and 52% of all resting sites (Table 3). Among resting sites used by males, the mean predicted probability of being a male resting site was 0.653, and among female resting sites, the mean probability of being a male resting site was 0.616 (Table 3). Because there was no significant model of male *versus* female resting sites during summer, and assessments of model fit and prediction were poor during winter, we combined males and females in subsequent logistic regression models to evaluate whether martens selected resting sites based on measures of forest overstory, understory, or ground structure.

During summer, the following variables were significantly different ($P < 0.10$) in univariate comparisons between resting sites ($n = 70$) and random sites ($n = 150$): overhead cover, foliage density < 0.5 m, foliage density 0.5-2.0 m, and number of coniferous stems. The stepwise logistic regression procedure resulted in a significant model ($P < 0.001$), with significant negative effects for overhead cover ($P < 0.001$) and foliage density <0.5 m ($P < 0.001$), and a positive effect for the dummy variable for canopy height >18 m ($P = 0.017$, Table 2). The model fit was fair (McFadden's rho-squared = 0.197), and the jackknife procedure correctly classified 39% of resting sites, 89% of random sites, and 73% of all sites (Table 3). Among resting sites, the mean predicted probability of being a resting site was 0.459, and among random sites, the mean predicted probability of being a resting site was 0.248 (Table 3).

Table 2. Logistic regression models of forest overstory, understory, and ground structure characteristics at marten resting sites in north-central Maine, 1991-1994.

				95% CI on odds ratio	
Variable	Coefficient	*P*-value	Odds ratio	Lower	Upper
Model: male (response) vs. female, winter[a]					
Foliage density <0.5 m	-0.344	0.045	0.709	0.507	0.993
Model: resting sites (response) vs. random sites, summer[b]					
Canopy height 1	-0.415	0.452	0.660	0.223	1.949
Canopy height 2	-0.270	0.473	0.763	0.365	1.596
Canopy height 3	1.122	0.017	3.071	1.220	7.730
Overhead cover	-0.035	<0.001	0.966	0.948	0.983
Foliage density <0.5 m	-0.789	<0.001	0.454	0.332	0.622
Model: resting sites (response) vs. random sites, winter[c]					
Coniferous stems	0.071	0.011	1.074	1.017	1.134
Snags	-0.601	0.005	0.548	0.359	0.838

[a] 41 male and 23 female resting sites. The model for sex-specific differences during summer contained no significant effects.

[b] 70 resting sites, 150 random sites.

[c] 64 resting sites, 51 random sites.

In univariate comparisons between resting sites ($n = 64$) and random sites ($n = 51$) in winter, the following variables were significantly different ($P < 0.10$): foliage density < 0.5 m, number of coniferous stems, and number of snags. The stepwise logistic regression procedure resulted in a significant model ($P < 0.001$), with a significant positive effect for number of coniferous stems ($P = 0.011$) and a negative effect for number of snags ($P = 0.005$, Table 2). The model fit was fair (McFadden's rho-squared = 0.123), and the jackknife procedure correctly classified 75% of resting sites, 47% of random sites, and 63% of all sites (Table 3). Among resting sites, the mean predicted probability of being a resting site was 0.615, and among random sites, the mean predicted probability of being a resting site was 0.484 (Table 3).

Table 3. Fit of logistic regression models of forest overstory, understory, and ground structure characteristics at marten resting sites in north-central Maine, 1991-1994.

	Predicted outcome[a]		Probability of response[b]	
Response variable	No. correct	% correct	mean	SD
Model: male (response) vs. female, winter[c]				
Male	33	80	0.653	0.136
Female	0	0	0.616	0.105
All	33	52		
Model: resting sites (response) vs. random sites, summer[d]				
Resting site	27	39	0.459	0.262
Random site	133	89	0.248	0.181
All	160	73		
Model: resting sites (response) vs. random sites, winter[e]				
Resting site	48	75	0.615	0.185
Random site	24	47	0.484	0.182
All	72	63		

[a] Frequency and percent of responses correctly classified by a jackknife procedure.

[b] Probability of response based on a jackknife model.

[c] 41 male and 23 female resting sites. The model for sex-specific differences during summer contained no significant effects.

[d] 70 resting sites, 150 random sites.

[e] 64 resting sites, 51 random sites.

Discussion

Martens on our study site used a variety of resting sites during both summer and winter. During summer, most resting sites were in trees or snags. Among resting sites in trees, spruce was the most commonly used species; however, the relative availability of individual tree species on the study site was unknown, and thus, relative selection of tree species cannot be inferred from our data. Whereas other studies in the eastern United States (Mech and Rogers 1977, Masters 1980, Steventon and Major 1982, Wynne and Sherburne 1984) have reported no use of

snags during summer, the finding that 22% of 73 summer resting sites on our study site were in snags is consistent with some studies in the western United States (Martin and Barrett 1983, 1991; Spencer 1987). The use of snags may vary with the relative abundance of alternative resting sites (Martin and Barrett 1983). Some summer resting sites (32% of 73 resting sites) occurred on or beneath the ground. Use of subterranean resting sites in summer may result from behavioral thermoregulation (Buskirk et al. 1988) on cool days during the period we defined as summer (1 May to 31 October), or may reflect the use of subterranean sites for maternal ground dens (Wynne and Sherburne 1984; D. J. Harrison, unpublished data).

During winter, martens also used a variety of resting sites; however, almost all were beneath the snow surface. Deep snow often prevented us from describing the structural characteristics of subnivean resting sites. Martens tended to rest in trees or snags during summer, and in subterranean or subnivean sites during winter. This pattern is consistent with evidence from other studies (Steventon and Major 1982, Buskirk 1984, Spencer 1987, Martin and Barrett 1991, Wilbert 1992), suggesting that thermoregulation (Buskirk et al. 1988) is important in resting-site choice.

We documented a relationship between ground structure and forest type; coniferous stands had more coniferous stems <7.6 cm in diameter, logs, and snags than deciduous stands, and more logs and snags than mixed stands. Regenerating conifers, logs, and snags have all been documented to provide opportunities for subnivean access (Corn and Raphael 1992); therefore, we conclude that opportunities for subnivean access increased as the coniferous component of stands increased. However, martens exhibited no apparent selection among deciduous, coniferous, or mixed forest types for resting, despite the fact that densities of logs and snags tended to increase as the coniferous component of stands increased. This pattern is consistent with the findings of Chapin et al. (1997); based on radio-telemetry data from 38 resident adult (≥1 year) martens on our study site, he concluded no difference in selection among deciduous, coniferous, and mixed stands relative to availability within home ranges.

The lack of selection by resting martens for forest type in either summer or winter is consistent with the hypothesis that, throughout our study site, availability of resting sites was greater than structural thresholds below which resting sites limit habitat use by martens. Despite the effect of forest type on ground structure, availability of potential resting sites may have been adequate in all forest types, and some other limiting factor may have determined habitat use, such as prey availability. Similarly, Thompson and Colgan (1994) documented that, despite greater access to subnivean spaces in unlogged areas *versus* logged areas, martens hunted beneath the snow at the same rate in both areas. In contrast, Buskirk et al. (1989) documented that martens in Wyoming selected for spruce-

fir stands over lodgepole pine (*Pinus contorta*) for resting, and suggested that the amount of ground structure was greater in spruce-fir stands than in lodgepole pine stands. They concluded that martens exhibited selection of forest types for resting because the habitat on their study site was patchy and because resting sites were not uniformly available. Contrary to our study site where potential resting sites did not appear to be limiting, potential resting sites on their study site may have occurred below thresholds that limited habitat use in the lodgepole pine stands that martens selected against.

Using logistic regression models, we noted few significant differences in measurements of forest overstory, understory, and ground structure between resting sites and random sites. Although the models for both summer and winter were significant, few variables had significant effects, and the models poorly predicted locations as resting sites or random sites. During summer, canopy height had a significant positive effect and overhead cover and foliage density had significant negative effects on the likelihood of a site being a resting site rather than a random site. Although most resting sites (90%) and random sites (87%) were in forest stands >12 m in height, more resting sites (27%) were in forest stands >18 m in height than random sites (6%). Canopy height may be related to tree bole diameter, which has been suggested in other studies to be an important determinant in the use of trees as resting sites (Wynne and Sherburne 1984; Spencer 1987; Martin and Barrett 1991; Raphael and Jones, this volume). Increases in overhead cover and foliage density <0.5 m decreased the likelihood that a site was used for resting. This result is contrary to published reports that martens select for stands with the greatest overhead cover (Koehler and Hornocker 1977, Soutiere 1979, Spencer et al. 1983, Bateman 1986), and may reflect selection by resting martens for residual trees in stands regenerating from spruce-budworm mortality (Chapin et al. 1997).

In winter, the number of coniferous stems had a significant positive effect on the likelihood of a site being a resting site *versus* a random site. Similarly, Corn and Raphael (1992) reported that small, live conifer trees, and not large, dead-wood structures, were the most commonly used subnivean access points in deep snow. Regenerating conifers not only provide subnivean access, but in dense clusters may also facilitate subnivean travel by intercepting snowfall and creating continuous subnivean spaces.

Although the logistic regression models were significant in both summer and winter, and identified effects with odds ratios significantly different from 1, assessments of model fit (McFadden's rho-squared < 0.2, poor classification rates, and mean probability of response close to 0.5) suggest that selection for the habitat features we measured was universally weak. Further, the lack of differences in many measurements of forest overstory, understory, and ground structure between resting sites and random sites in both summer and winter, in both

univariate and multivariate tests, suggests that, throughout our study site, potential resting sites may not be limiting. Evidence suggests that marten may be opportunistic in their choice of resting sites (Martin and Barrett 1983; Thompson and Colgan 1994; Raphael and Jones, this volume), thus the relative abundance of potential resting sites may dictate which sites are used. Another potential explanation of our results is that martens responded to qualitative aspects of habitat that we did not measure (Hobbs and Hanley 1990). For example, the size and decay class of logs on the forest floor, in addition to their abundance, may be important in determining their use by resting martens (Corn and Raphael 1992).

In the mosaic of mesic, second-growth forests within the eastern portion of the range of the American marten, vertical and horizontal structure may occur above thresholds required for resting, regardless of whether stands are dominated by deciduous or coniferous trees. Forests across the range of the American marten differ in structure, species composition, natural disturbance regimes, and management. Therefore, an understanding of region-wide mechanisms of habitat use are required for range-wide descriptions of habitat associations.

Management Implications

The recent disturbance history on our study site (i.e., spruce-budworm infestation, fire, and timber harvesting by humans) has resulted in a mosaic of forest ages and cover types. Although structural characteristics of forest types on our study site differ, our results suggest that availability of structure used for resting was greater than thresholds below which resting sites limit the use of habitat by martens. This suggestion implies that, assuming such thresholds exist and are measurable, forests can be managed to provide adequate amounts of this important requirement of the marten (Raphael and Jones, this volume). Some current silvicultural practices (e.g., whole-tree harvesting, short rotations, herbiciding) in the eastern sub-boreal Acadian forest occupied by the marten have the potential to reduce vertical and horizontal forest structure in the long term (Harmon et al. 1986, Lansky 1992, Seymour and Hunter 1992). Therefore, we recommend further study to document quantitative and qualitative thresholds of forest structure at which resting sites limit use of habitat by martens, and to examine the influence of current timber harvesting trends on long-term forest structure.

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STAND STRUCTURE AND MICROTINE ABUNDANCE IN NEWFOUNDLAND: IMPLICATIONS FOR MARTEN

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Abstract: The meadow vole (*Microtus pennsylvanicus*), which is normally associated with open habitats, is the only microtine found in Newfoundland and one of the few prey items available to American marten (*Martes americana*) on the island. Meadow voles were sampled within "immature," "semimature," "mature," and "overmature" coniferous stands in western and central Newfoundland during 1993 and 1994. Voles were most abundant in "overmature" stands ($P \leq 0.05$). Further, vole abundance was negatively correlated with both relative tree density (a quantitative measure of tree competition within a stand) and the availability of dead and downed coarse woody debris. Results suggest that voles respond to the changes in stand structure associated with stand senescence. Generalizations regarding marten habitat requirements that are based on studies at mainland sites may not be applicable to the unique depauperate prey conditions of Newfoundland.

Introduction

American martens (*Martes americana*) are commonly found within older successional spruce-fir and mixed coniferous habitat (Mech and Rogers 1977, Soutiere 1979, Spencer et al. 1983, Buskirk 1984, Bissonette et al. 1989, Thompson 1994). This association is remarkably consistent across its entire range. In addition, as a predator that requires large areas of relatively contiguous habitat, the marten is considered to be a reasonable indicator of the integrity of older coniferous forest systems. The similarity in marten behavior and requirements across regions allows land managers to develop local marten management plans based on information from a wide variety of sources. However, managers must be cognizant of local ecological processes that may influence marten response to different habitat management regimes.

Table 1. Availability within Newfoundland of potential marten prey species that occur at the same latitude on the eastern Canadian mainland (Burt and Grossenheider 1980).

	Newfoundland prey species	
Prey species	Found in isolated pockets	Distributed throughout marten range
Meadow vole (*Microtus pennsylvanicus*)	X	X
Boreal redback vole (*Clethrionomys gapperi*)		
Mountain phenacomys (*Phenacomys intermedius*)		
Yellownose vole (*Microtus chrotorrhinus*)		
Deer mouse (*Peromyscus maniculatus*)	X	
Meadow jumping mouse (*Zapus hudsonicus*)		
Woodland jumping mouse (*Napaeozapus insignis*)		
Starnose mole (*Condylura cristata*)		
Northern bog lemming (*Synaptomys borealis*)		
Southern bog lemming (*Synaptomys cooperi*)		
Masked shrew (*Sorex cinereus*)	X	X
Northern water shrew (*Sorex palustris*)		
Pygmy shrew (*Sorex hoyi*)		
Shorttail shrew (*Blarina brevicauda*)		
Northern flying squirrel (*Glaucomys sabrinus*)		
Snowshoe hare (*Lepus americanus*)	X	X
Red squirrel (*Tamiasciurus hudsonicus*)	X	
Eastern chipmunk (*Tamias striatus*)	X	

The depauperate prey base on the island of Newfoundland presents a unique ecological situation for marten. Table 1 contrasts the Newfoundland prey situation with the typical array of prey species available to marten in eastern Canada at the same latitude. In general, prey species common on the mainland are not found in Newfoundland. Furthermore, half of the species present on the island are recent introductions, and are therefore only locally available (Tucker 1988, Thompson and Curran 1995). Hence, only three prey species are presently ubiquitous in Newfoundland forests. This condition may influence the distribution, size, and stability of local marten populations.

Voles are a staple food for marten across its range (Martin 1994); yet only the meadow vole (*Microtus pennsylvanicus*), a species normally associated with open habitats (Getz 1970, Grant 1971, Folinsbee et al. 1973, Geier and Best 1980, Galindo and Krebs 1985), is found in Newfoundland. Tucker (1988) demonstrated that meadow voles were the most important prey item for marten within a region of old-growth forest in Newfoundland, whereas Bateman (1986) found that voles were second to snowshoe hare in percent frequency of occurrence in scats during winter. Given the paucity of alternative prey species, marten habitat quality in Newfoundland is likely influenced by meadow vole distribution within forested environments (Thompson and Curran 1995).

Typical meadow vole habitat is characterized by open, mesic locations supporting abundant graminoid vegetation (Getz 1970). Dense grasses provide not only a source of food, but also the structure necessary for the construction of protective runways (Birney et al. 1976). The shading effect of tree canopies within forests tends to inhibit understory growth, providing at least a partial explanation for the low densities of meadow voles found within this habitat type. Indeed, past studies have shown a general increase in meadow vole abundance after tree removal (Kirkland 1990). It follows that factors (e.g., canopy closure) that affect the growth of ground-level vegetation should influence meadow vole abundance within forested stands.

A useful method of characterizing stand structure is "relative density," which is a quantitative measure that evaluates the degree of competition between trees within a stand (Drew and Flewelling 1977). Relative density is essentially a packing ratio that relates the mean volume of trees to the density of stems, as a function of the self-thinning rule (Drew and Flewelling 1977). Specifically, above a certain threshold density for a given average stem size, the limited resources cannot support all trees present, causing mortality in stressed trees (i.e., self-thinning). The range of relative densities where self-thinning occurs is defined as the Zone of Imminent Competition Mortality (ZICM) (Drew and Flewelling 1977). Newton and Weetman (1993) calculated the ZICM for black spruce in central Newfoundland as those stands falling between a relative density of 0.5 and a maximum index value of 1.0.

Stands within ZICM are typically very dense, with high canopy closure and sparse understories. If left unmanaged, regenerating stands generally maintain themselves within the ZICM. However, as a stand begins to senesce into what Oliver and Larson (1990) described as a "transition old-growth" state, mortality occurs at a faster rate than the remaining trees can use the released resources (i.e., light, water, nutrients). Agencies interested in timber or pulpwood production often classify stands within this stage as "overmature", because standing tree volume begins to decrease over time (D. Harris, pers. commun.). However, as dominant and codominant trees die and fall to the ground, the overstory canopy

opens, and the complexity of both the physical structure (e.g., fallen logs, root masses) and the plant community increases within the forest understory (Oliver and Larson 1990, Sturtevant 1996). Because meadow voles are influenced by ground-level vegetation and structure, forest succession dynamics will likely affect vole abundance within forest stands in Newfoundland.

Although the typical habitat associations of meadow voles on the mainland have been well documented, their specific habitat requirements within forested systems are not well understood. We measured the relative abundance of small mammals during the summers of 1993 and 1994 within "semimature," "mature," and "overmature" coniferous stands in western Newfoundland, and "immature" and "overmature" stands within central Newfoundland. We report microtine-capture success by stand type, and relate the observed relationship between stand age and vole abundance to the structural characteristics of these forest types. Finally, we discuss the implications of our results to the management of marten on the island of Newfoundland.

Study Areas

We collected small mammal data from two widely separated locations on the island. Study areas were selected based on the range of age classes available, and the presence of marten in the area. The South Brook study area was located approximately 20 km east of the town of Corner Brook in western Newfoundland (Forest Section B28b of the Canadian Boreal Forest Region; Rowe 1972). The Victoria Lake study area was located approximately 100 km east of the town of Stephenville in the western-most section of the central region of Newfoundland (Forest Section B28a of the Canadian Boreal Forest Region; Rowe 1972).

Newfoundland is characterized by a wet, cool climate, with an annual temperature averaging 4°C (Banfield 1983). Forest composition of each study area was similar. Balsam fir (*Abies balsamea*) dominated all study sites, and black spruce (*Picea mariana*), white spruce (*P. glauca*), and white birch (*Betula papyrifera*) also were common overstory species. The understory plant communities ranged from moss- (e.g., *Hylocomium splendens*, *Pleurozium schreberi*) to herb-dominated (e.g., *Ribes* spp., *Viburnum* spp., *Streptopus* spp.) (Meades and Moores 1994). Small spruce fens (0.1-0.5 ha) were interspersed throughout most forested stands. Additionally, periodic defoliation by spruce budworm (*Choristoneura fumiferana*) and hemlock looper (*Lambidina fiscellaria*) has opened the canopy of some of the more mature stands (Thompson 1991).

The Corner Brook mill began logging in the South Brook valley as early as 1924, with the greatest portion harvested in the 1940's (Horwood 1986). The additional presence of residual stands provided three age classes of forest: semimature (40-60 years), mature (60-80 years), and overmature (80+ years). In

contrast, tree harvest within the Victoria Lake study area occurred between the late 1950's and the late 1960's (Abitibi-Price, Inc., company records). A few inaccessible stands of trees remained unharvested. Only two age classes were available within the Victoria Lake study area. They were immature (20-40 years) and overmature. All of the stands sampled were naturally regenerated, and none had been subjected to post-harvest silvicultural treatments (i.e., herbicides, pre-commercial thinning, etc.).

Methods

Small Mammal Data

The 1993 trapping design was intended to describe differences in the relative abundance of small mammals within semimature, mature, and overmature (unharvested) stands. We selected three stands within each age-class using forest inventory maps provided by the Newfoundland Department of Forestry. Standard 7 × 7 or 6 × 6 removal trapping grids were established according to Kirkland (1982), using a 15-m spacing between stations. Two Victor snap traps were used at each station. Traps were baited with peanut butter and set for four consecutive nights. The first trapping session was conducted in July 1993. All trapping grids were then moved 50-200 m from the first trap site to ensure that the initial removal of animals did not influence harvesting success during the second trapping session, which was conducted from mid- to late August.

Preliminary examination of 1993 capture data and observations from the field suggested that there was a fair degree of habitat heterogeneity within stands due to small patches of residual trees, insect defoliation, and interspersion of spruce fens. To account for this within-stand variability, we altered our study design in 1994 (Fig. 1), and included an immature age-class. A minimum of two stands were selected for each age-class available within each study area. Fifteen to 20 sample plots were placed at 50-m intervals along a predetermined transect within each stand. Each plot was established for collecting forest structure data as described below. Six "mini-grids" (2 × 8) were placed within each site, and spaced uniformly along the transect (Fig. 1). Grids were spaced a minimum of 50 m apart. Three grids per site were set during each trapping session, and we followed the same protocols for baiting and trapping as in 1993. Small mammal abundance was reported as the number of animals trapped per 100 trap-nights (Getz 1982). We corrected for sprung traps in our calculation of trapping results (Nelson and Clark 1973).

Stand Mensuration

Measurements of stand structure were taken at 4 uniformly spaced plots within the 1993 trap grid locations, and the same measurements were taken at two

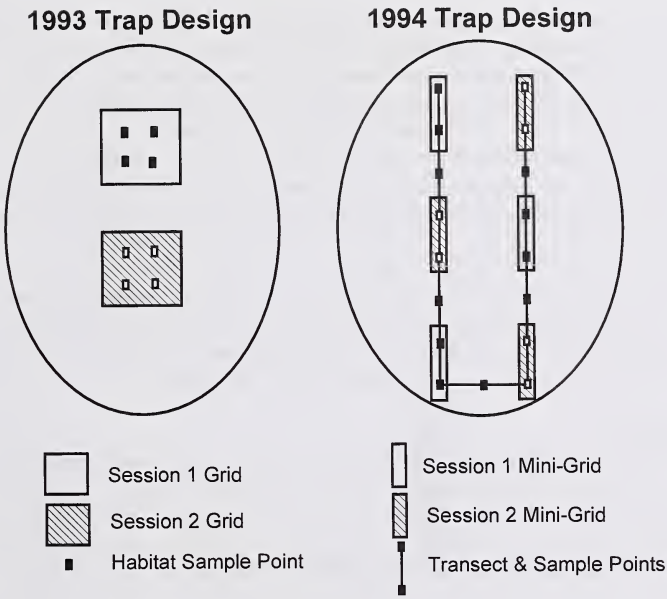

Figure 1. Study design changes from 1993 to 1994. The ellipses represent stand boundaries.

plots within each 1994 mini-grid location (Fig. 1). Standing trees were measured using a variable radius sample-plot methodology (i.e., trees were tallied using a prism, and diameters of all "in" trees were measured to the nearest cm; Husch et al. 1972). Two random trees per plot were aged using cores extracted at breast height with an increment borer. For the 1993 grids, sample ages were averaged to estimate individual grid age. Because the 1994 trapping design was intended to assess vole abundance at the stand level, sample ages were averaged across mini-grids as an estimate of overall stand age. An additional dominant tree (by crown class) was aged and measured for height (± 0.25 m) using a clinometer. The age of each tree was determined by adding 8 years to the age determined from the increment cores. Eight years is the estimated time for a tree to reach breast height (D. Harris, pers. commun.).

Relative density was calculated by first using dominant tree heights measured at each plot to calculate individual tree heights using Page and van Nostrand's (1973) height-diameter regression functions. Volumes were then calculated using

Warren and Meades's (1986) taper equations. Stem density and volume estimates were calculated for each plot using Husch et al.'s (1972) methodology for variable-radius sample plots. We then employed a preliminary relative density index equation provided by Newton (Forestry Canada, unpubl. data) for balsam fir-black spruce stands in Newfoundland (Sturtevant 1996).

The amount of dead and downed woody debris was also measured within each plot because of both its significance to marten habitat quality, and its possible function as ground-level protective cover for voles. Downed logs were measured using a modified version of Brown's (1974) planer intersect method. A 20-m long tape was extended from a sample point in a random direction. Logs > 7.6 cm in diameter intersecting the vertical plane defined by the tape were measured for diameter at the point of intersection. Finally, each plot was stratified into forest ecosystem types based on the plant species present, topography, and soil type, as a measure of site potential (Meades and Moores 1994).

Analysis

Because of the potential for population differences between study areas, we analyzed small mammal data from Victoria Lake and South Brook separately. Hence, because only overmature sites were trapped in the Victoria Lake study area in 1993, data obtained from these sites were used for comparative purposes only. An examination of tree ages from 1993 trapping grids suggested that residual tree patches within stands inflated the overall age of trees in localized areas where certain trap grids were placed. The objective of this study was to determine the effect of forest age on vole abundance; samples were therefore reclassified into the *a priori* age classes according to actual grid age, not the stand age. Trapping over 2 sessions yielded 4 semimature, 5 mature, and 5 overmature samples for the 1993 analysis. The 1994 trapping design allowed for spatial variation within stands by using multiple samples during each session; we therefore analyzed 1994 data using the overall stand age.

Relative abundance data were log transformed (Sokal and Rohlf 1981). We used an analysis of variance (ANOVA) to test differences between age classes and between sessions. A *t*-test was used for comparisons between individual second-growth age classes and the overmature age class (Sokal and Rohlf 1981). Pearson's product-moment coefficient (ρ) was used to determine the extent of correlation between vole abundance and habitat variables (Sokal and Rohlf 1981).

Results

Vole abundance within the forest was generally low; a trapping effort of 14,864 trap nights over 2 years yielded a total of 211 voles. However, vole abundance

differed significantly ($P \leq 0.05$) between age classes; the majority of voles were captured in overmature locations (Fig. 2). Results from the South Brook study area in 1993 show that both semimature and mature stands had significantly ($n = 14$, df = 2, $F = 5.64$, $P = 0.03$) lower vole abundance than overmature stands. No difference was detected between trap sessions (df = 1, $F = 0.63$, $P = 0.45$), and no interaction was observed (df = 2, $F = 0.677$, $P = 0.528$). Differences in trapping design between years did not allow a direct comparison of vole population trends. However, a drastic decline in vole abundance was noted for South Brook

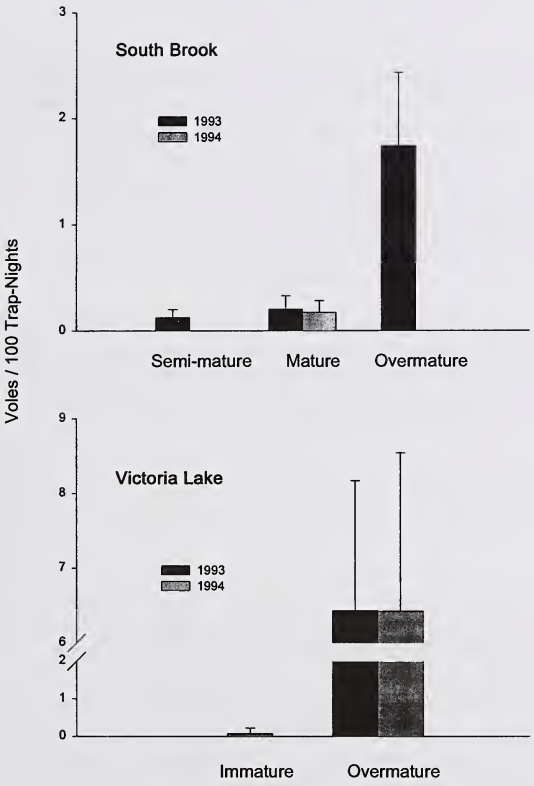

Figure 2. Meadow vole distribution among forest age classes; comparison of semimature, mature, and overmature classes at the South Brook study area, and comparison of immature and overmature classes at Victoria Lake study area. Error bars are standard errors.

in 1994; only 2 voles were captured in 5376 trap-nights (0.03/100 TN). Analysis of 1994 data was therefore not possible.

Abundance differences were even more profound between immature and overmature stands. In total, 93 voles (6.14/100 TN) were captured in the overmature stands within the Victoria Lake study area, whereas only 1 vole (0.07/100 TN) was captured in immature stands with the same trapping effort (Fig. 2). Although these data violate the homogeneity of variance assumption of the analysis of variance (Sokal and Rohlf 1981), the relationship is clearly significant. Notably, the sharp decline in vole abundance observed within the South Brook study area was not observed at Victoria Lake.

Tables 2 and 3 show the structural characteristics of measured grid sites and stands, respectively. In general, second-growth stands had higher relative tree densities and lower volumes of coarse woody debris (CWD) than overmature stands. In stands greater than 40 years of age (1993 South Brook data), the relative density of standing trees appeared to have a negative influence on vole abundance ($n = 14$, $r = -0.682$, $P = 0.007$). Vole abundance was also positively correlated with CWD ($n = 14$, $r = 0.783$, $P = 0.001$).

Discussion

The results of this study suggest that meadow voles within the forests of Newfoundland are influenced by stand structure. This relationship is reflected in the distribution of voles among forest age-classes; voles were significantly more abundant in overmature locations than all other forest age-classes.

In Newfoundland's balsam fir-dominated forests, stand dynamics following clearcut harvesting are characterized by relatively rapid balsam fir regeneration, followed by intense intertree competition (i.e., high relative density). These self-thinned stands maintain "relative densities" within the ZICM until stand senescence (Sturtevant 1996). The majority of voles captured in this study were captured in locations falling outside the ZICM (Fig. 3). This relationship is largely independent of age; overmature sites within the ZICM also had low vole abundance. Hence, the relationship between vole abundance and forest age likely reflects the increased probability that older stands contain locations in various stages of senescence.

Thompson and Curran (1995) suggested that meadow voles were rare in second-growth forests of Newfoundland because of the lack of available understory. Our results agree with this hypothesis. At present, most second-growth stands in Newfoundland have not yet reached the "transition old-growth" (i.e., "overmature" or "senescent") state described by Oliver and Larson (1990). Hence, the dense tree canopies of second-growth stands reduce the light available for understory plant development. Monthey and Soutiere (1985) found that meadow voles

Table 2. Stand structure summary for trap grid locations in 1993. Values are mean estimates based on 4 sample plots taken within each vole trap grid. (See text for explanation).

Grid	Location[a]	Age class	Session	Basal area (m^2/ha)	Density (trees/ha)	Site index (m)[b]	Relative density[c]	Fallen logs (m^3/ha)
31	SB	semimature	1	48.2	4532.5	14.7	0.62	9.4
51	SB	semimature	1	53.9	3306.2	15.4	0.64	23.5
32	SB	semimature	2	50.5	6443.2	14.7	0.69	0.0
42	SB	semimature	2	41.3	5582.1	14.5	0.56	14.9
41	SB	mature	1	57.4	2062.8	14.4	0.68	47.5
61	SB	mature	1	59.7	5421.5	15.4	0.84	11.6
62	SB	mature	2	41.3	1845.1	15.2	0.50	23.8
71	SB	mature	1	37.8	2734.5	14.6	0.56	10.2
72	SB	mature	2	57.4	3626.5	14.6	0.74	7.7
52	SB	overmature	2	33.3	926.3	15.4	0.36	66.2
81	SB	overmature	1	28.7	934.4	15.2	0.37	51.5
82	SB	overmature	2	35.6	1600.0	15.2	0.46	13.2
91	SB	overmature	1	59.7	2758.9	15.2	0.71	58.3
92	SB	overmature	2	48.2	1140.0	16.8	0.33	102.5
11	VL	overmature	1	11.5	539.0	12.2	0.13	95.7
12	VL	overmature	2	32.1	1959.9	12.5	0.37	28.0
21	VL	overmature	1	25.3	4977.0	12.2	0.57	42.2
22	VL	overmature	2	27.5	5021.7	11.5	0.43	31.2

[a] SB = South Brook; VL = Victoria Lake.

[b] Values derived from the Forest Ecosystem Classification system for Newfoundland (Meades and Moores 1994).

[c] Relative Density Index (no units).

Table 3. Stand structure summary for stands sampled in 1994. Values are mean estimates based on 12-20 sample plots taken within each stand sampled for voles. (See text for explanation).

Site (stand)	Location[a]	Age class	Session	Basal area (m^2/ha)	Density (trees/ha)	Site index (m)[b]	Relative density[c]	Fallen logs (m^3/ha)
14	VL	immature	1,2	22.1	11,371.6	12.0	0.33	31.6
15	VL	immature	1,2	36.7	22,210.0	13.2	0.56	43.1
1	VL	overmature	1,2	18.0	1066.1	13.2	0.22	64.4
20	VL	overmature	1,2	33.5	3043.5	11.7	0.45	26.0
3	SB	semimature	1,2	49.1	5002.2	14.1	0.62	17.3
4	SB	semimature	1,2	38.6	4742.8	14.8	0.52	29.2
22	SB	semimature	1	40.9	3298.5	15.0	0.52	49.8
6	SB	mature	1,2	38.9	2754.2	13.5	0.51	54.6
23	SB	mature	1	34.0	1539.1	14.8	0.43	46.0
8	B	mature	1,2	33.0	1484.4	14.8	0.43	78.1
17	SB	overmature	1,2	31.5	1661.7	14.7	0.42	65.2
9	SB	overmature	1,2	36.0	3904.8	12.8	0.48	54.9

[a] VL = Victoria Lake; SB = South Brook.

[b] Values derived from the Forest Ecosystem Classification system for Newfoundland (Meades and Moores 1994).

[c] Relative Density Index (no units).

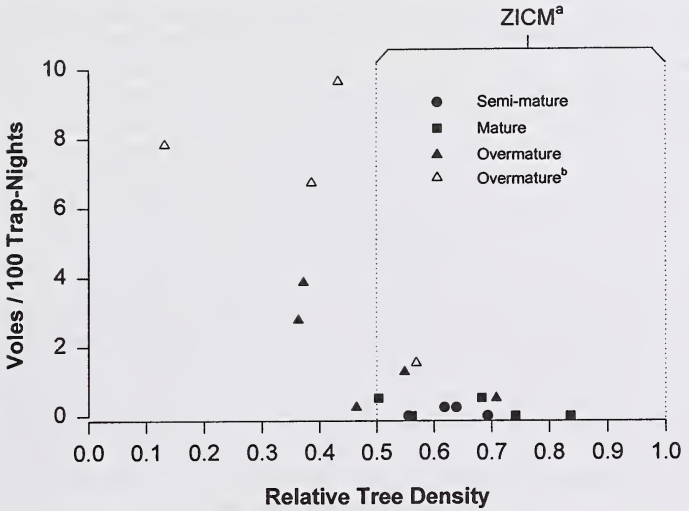

Figure 3. Meadow vole response to forest structure in 1993 ([a] Zone of Imminent Competition Mortality; [b] Victoria Lake sites not included in analysis, see text).

were rare in uncut softwood stands in Maine, but more abundant within partially cut and clearcut stands in that region. Swan et al. (1984) reported similar results within hardwood forests of Nova Scotia. Each study attributed higher vole abundance to the increased understory plant growth, which they attributed to canopy thinning or removal.

Furthermore, senescent stands typically have large amounts of dead and downed CWD (Sturtevant 1996). Birney et al. (1976) stressed the importance of vegetative structure necessary for the construction of protective runways and subnivean conduits. Downed logs may also provide similar structure in forested environments, where dense grass is typically unavailable (Thompson and Curran 1995). A study of a similar species, *Microtus longicaudus*, suggests that microtines may congregate around fallen logs underneath the snowpack (Spencer et al. 1983).

Implications for Marten

The observed relationships indicate that certain assumptions of marten habitat quality may not apply to the unique ecological situation on the island of Newfoundland. Overhead cover is commonly expressed in the literature as a

major factor influencing marten habitat suitability (Hargis and McCullough 1984, McCallum 1992). Allen's (1982) Habitat Suitability Index model for marten assumes overhead cover greater than 50% is optimal, and local marten habitat management plans stress the importance of high canopy closure (e.g., Beaudette 1991). Our data indicate that meadow voles are virtually nonexistent within very dense stands, suggesting that the maintenance of contiguous, dense conifer forests could potentially be detrimental to Newfoundland marten. Although many studies suggest small openings may be beneficial to marten by increasing prey abundance (e.g., Koehler et al. 1975, Spencer et al. 1983), the relative importance of this phenomenon may be amplified in Newfoundland due to the rather specific habitat requirements of the main prey species.

Further, tree defoliation as a result of insect epidemics is often perceived as detrimental to marten habitat because of substantial canopy loss. Yet defoliated areas often retain a high degree of standing structure for over a decade after the initial disturbance (Ostaff and MacLean 1989). Defoliated patches may serve as short-term reservoirs for microtines within a forested environment. Tracking data from marten in old-growth forest (Drew 1995) indicate that marten in Newfoundland select defoliated areas as foraging sites. Our observations of marten in second-growth forests support this hypothesis.

Most marten biologists agree that marten habitat quality improves with the successional stage of the forest (see Buskirk et al. 1994). Several mechanisms have been implicated as the cause of this close association, including thermal constraints (Buskirk 1984, Buskirk et al. 1989), energetic requirements (Hargis and McCullough 1984, Bissonette and Sherburne 1994), and predator avoidance (Thompson 1994, Drew 1995). As a subspecies, the Newfoundland marten is probably not very different from its mainland counterpart, and must operate under the same physiological and behavioral constraints. What makes Newfoundland unique is the low diversity of available prey species. Our results indicate that voles become very scarce when tree canopies are closed, and do not increase significantly in abundance until the stand begins to senesce into a "transition old-growth" state (Oliver and Larson 1990). Although other regions may also observe a general increase in the abundance of small mammals in overmature or old-growth forests (e.g., Raphael 1984), the distinction between mature and overmature forests may not be as acute in areas with a full array of small mammal prey species.

Marten populations on the mainland appear to have a much greater chance of surviving the crash of an individual prey species by switching to alternate prey. Observations from the present study and others on the island (Tucker 1988) suggest that microtine populations are volatile in Newfoundland. The effect on the resident marten population may be profound (Tucker 1988).

Hence, generalizations of marten habitat requirements developed from marten research throughout mainland North America may not apply to the local conditions of Newfoundland. The depauperate prey base, specialized habitat requirements of available prey, and fluctuating microtine population creates a very fragile system that may be particularly sensitive to human disturbance. Consequently, any management plan that includes marten habitat as an objective must recognize the constraints imposed by the available prey resource.

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INTERACTIONS AMONG MARTEN PREY AVAILABILITY, VULNERABILITY, AND HABITAT STRUCTURE

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Abstract: Prey density is important to the American marten (*Martes americana*), but prey vulnerability may be just as important. We were able to investigate the association between marten habitat use, prey density, dynamics of prey populations, and structural complexity of vegetation during a study of martens in 2 areas of southwest Montana during 1989-1992. Twelve radio-collared martens used sites in the Upper Big Hole ($n = 197$) and West Yellowstone ($n = 120$) with higher structural complexity indices (ground cover + tree cover + shrub cover + downfall cover) than locations selected at random. Red-backed vole (*Clethrionomys gapperi*) capture rates in spring and fall were strongly associated with high structural complexity (Spearman rank correlation = 0.83, $P < 0.01$) whereas deer mouse (*Peromyscus maniculatus*) capture rates were not (Spearman rank correlation = 0.33, $P = 0.32$). Vole capture rates during the spring and fall for habitats used by radio-collared martens during winter were higher ($t = 3.66$, $P < 0.01$) than capture rates at sites in habitats not used by marten during winter. Capture rates for total rodents and deer mice did not differ ($t = 1.21$ and 0.64, respectively; $P > 0.25$) between habitats used by martens and habitats that were not. Capture rates for total small mammals, voles, and deer mice in summer tended to be higher in habitat types used by martens in winter. Survivorship of deer mice in summer tended to be higher in habitat types used by martens in winter. Survival of deer mice and red-backed voles did not differ over summer ($t = 0.69$, $P = 0.50$), but voles had higher recruitment rates ($t = 2.15$, $P < 0.10$). When survivorship and

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recruitment were used to calculate biomass loss over summer, we recorded the highest vole biomass losses in trapping grids located in 4 cover types used by martens in winter. Simply measuring prey density during non-snow periods alone may be misleading when trying to determine the availability of prey during winter if population dynamics of the species are not considered. Our results support the hypothesis that martens selected habitat in winter in our study areas based on the availability and density of vulnerable red-backed voles, rather than simply the density of small mammals.

Introduction

Generally, the American marten (*Martes americana*) in the Rocky Mountains prefers mature conifer stands that are characterized by downed woody material, a well-developed canopy, high tree basal area and herbaceous ground cover. These more structurally complex habitats are important to marten for resting (Buskirk 1984, Spencer 1987, Buskirk et al. 1989, Fager 1991, Kujala 1993, Coffin 1994) and foraging (Campbell 1979, Bateman 1986, Sherburne and Bissonette 1994) during winter.

Douglass et al. (1983) found that martens may select certain areas of the forest on the basis of the abundance and availability of prey rather than solely on the basis of the habitat structure. However, it has not been clearly shown what physical and/or biological mechanisms best predict the use of these habitats by martens.

Morphologically and physiologically, the American marten is not well adapted to winter climates of the northern Rocky Mountains (Scholander et al. 1950, Iverson 1972, Buskirk et al. 1988, Buskirk and Harlow 1989); this limitation results in a serious thermoregulatory dilemma for marten during winter. Martens compensate for these shortcomings through behavioral adaptations when resting and foraging. Resting martens have been shown to select sites that minimize energy losses (Buskirk et al. 1989). Foraging martens have been found to synchronize their activities with that of prey when temperatures are coldest (Zielinski et al. 1983). Because martens are morphologically and physiologically maladapted to winter climates and need several meals each day (Harlow 1991) to counter thermal energy losses during this period, they must use sites with access to a dependable food supply. Although all small and medium-sized mammals are potential prey, food-habits data (Aune and Schladweiler 1993) reveal higher frequencies of voles in the diets of the marten in Montana.

Martens can and do pursue prey above the snow, but a major resource, small rodents, is commonly found below the snow. Subnivean access is linked to the species composition of the rodent guild because different species use areas with different overhead and ground coverage. Martens are likely using part of this guild disproportionately because of this relationship. Our objective was to identify factors that may influence habitat selection by martens, specifically those factors associated with prey availability and vulnerability. We investigated the

associations among marten habitat use, prey density, dynamics of prey populations and structural complexity of vegetation during a study of martens in 2 areas of southwest Montana, USA, during 1989-1992.

Study Area

Our study was conducted in the Upper Big Hole and West Yellowstone study areas from September 1989 through September 1992. Because this study was part of a larger effort, the study areas were chosen based on historic marten harvests, proximity to large untrapped areas, representative habitat types, and supporting agency jurisdictions. The 153-km^2 Upper Big Hole study area was located 15 km west of Wisdom, Montana and immediately northwest of the Big Hole National Battlefield. Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) were the dominant tree cover on drainage bottoms and higher elevation sites. Drier and lower elevation sites supported lodgepole pine (*Pinus contorta*) and Douglas-fir (*Psuedotsuga menziesii*). Elevation ranged from 1950 to 2500 m. Annual precipitation at the town of Wisdom averages 30 cm, with an average temperature of 1.7°C (US Department of Commerce 1990). Timber has been harvested on 15% of the area since the late 1950's.

The West Yellowstone study area (64 km^2) was located approximately 230 km southeast of the Upper Big Hole study area and is situated in a high elevation basin (2000 m) in the extreme southern part of Montana. Average temperature at the town of West Yellowstone is 1.6°C (USDC 1990). A lodgepole pine/antelope bitterbrush (*Purshia tridentata*) habitat-type (Pfister et al. 1977) was the dominant vegetation in this area. Natural openings and clearcuts support vegetative cover dominated by grass species. Willow (*Salix* spp.) communities were scattered throughout the area primarily along perennial streams. Large-scale timber harvesting has taken place on the study area since the late 1950's with 37% of the study area having been harvested.

Methods

Marten Livetrapping

Martens were captured using Tomahawk single-door live traps from September through March of each year. Captured martens were anesthetized with 0.1-0.4 cc of ketamine hydrochloride (100 mg/ml) depending on the size of the animal. Time from injection to release was generally under 30 minutes. Immobilized martens were placed back in the trap after processing and held until they displayed behavior similar to that observed before being anesthetized. Each marten was equipped with a radio-collar (AVM Instrument Co., Livermore, California, or Telonics, Mesa, Arizona).

Martens were located diurnally each day between December and May during 1989-1992. Locations of collared martens were pinpointed (within 1 m) through ground searches using directional antennas until the marten was visually sighted or tracks disappeared under snow. Locations of collared martens were flagged so they could be relocated for habitat measurements during the summer. Martens were not tracked during the summer months because this period was used to collect habitat data based on winter sightings.

Marten Habitat Evaluation

Marten habitat use was based on winter locations of radio-collared martens (Kujala 1993, Coffin 1994). Habitat variables were measured at all locations where martens had been sighted and for randomly selected sites. Random sites where chosen from each square kilometer within the study areas using a random number chart to generate UTM coordinates. Habitat variables for marten locations were measured during the summers (May to August) of 1991 and 1992. Measurement of habitat variables followed a procedure developed by Fager (1991) for marten locations and random plots. These procedures were based on a modified timber stand exam (US Department of Agriculture 1985). All trees measuring >12.7 cm in diameter within a "variable radius" plot (Young and Giese 1990) were counted at each marten location. In variable radius plot sampling, an angle gauge is used to define the size of the plot and the number of "in trees." For this study the angle gauge had a basal area factor of 20 English units. The number of intercepts of downed woody material (DWM) ≥7.6 cm in diameter was determined using field methods described by Brown (1974). Specifically, counts were made along an 8.2-m long transect, which ran on an easterly bearing from the center of the plot. Percent cover of DWM, shrubs, grass, and non-vegetative cover (rock, bare ground) was estimated to the nearest 5% through ocular estimation within a circular plot with a radius of 3.5 m.

Habitat variables at winter marten locations were compared to random plots measured by Fager (1991) using *t*-tests (Box 1953, Boneau 1960). Values for habitat variables from marten locations that differed from those at random locations at the $P < 0.10$ level were considered significant and interpreted to mean animals were selecting for that variable.

Small Mammal Trapping

Small mammals were sampled in habitats that were used by martens and in habitats not used by martens during the winters of 1990-91 and 1991-92. Two different small mammal trapping schemes were used to sample a variety of habitats in different seasons. First, a single line of 50, or 2 parallel lines of 25, Sherman live-traps were placed in 11 different sites representative of habitats used and not used by martens during winter. Sites differed with respect to cover

type, ground cover, and structural characteristics such as DWM. Habitats used by martens that were sampled using this approach included the following: 2 subalpine fir types, 1 with a mesic soil moisture rating and 1 with a xeric soil moisture rating (Warren 1989); Douglas-fir; and lodgepole pine/graminoids. Habitats not used by martens included the following: 4 lodgepole pine types; 2 clearcut types; and a willow cover type. Lodgepole pine cover types were annotated with the dominant understory vegetation. This approach was used to sample several different cover types and to compare relative densities of small mammals before and after the winter months. Traps were baited with peanut butter and rolled oats and supplied with synthetic cotton for insulation. Rodent populations were sampled for 3 consecutive nights before winter snow cover and after snowmelt during the fall of 1990, spring and fall of 1991, and spring of 1992. Animals were identified to species, ear-tagged or toe-clipped, weighed, and released.

Our second trapping scheme involved 4 trapping grids (100 traps/grid) established in each study area. Two grids were set in each study area in habitats with structural characteristics used by marten, and 2 grids were set in habitats with structural characteristics not used by marten. These grids were placed in areas not sampled by the first scheme. Used cover types sampled with this method included spruce, subalpine fir, Douglas-fir, and a lodgepole pine/graminoid type. Unused cover types included 3 lodgepole pine types and a clearcut type. Again, each lodgepole pine type had a different understory vegetation. Small mammals were sampled at biweekly intervals for 3 consecutive nights for a total of 3 sampling periods each summer (July to September) in 1991 and 1992. Each grid was approximately 1 hectare in size (100 × 100 m) with 10 parallel rows and 10 traps per row. An enumeration technique described by Chitty and Phipps (1966) was used to determine minimum number alive (MNA), survival, recruitment, and rodent biomass (g) lost from the grids during the 2 summers. Biomass values were determined by summing the individual weights of rodents that were caught during the first sampling period and absent from the last sampling period. Biomass losses were totaled for the 2 summers. Availability was determined from capture rates. Vulnerability was assessed from biomass losses. As with the first scheme, captured animals were identifed to species, ear-tagged, weighed and released.

Capture rates (captures/100 trap nights) for deer mice (DM), red-backed voles (RBV) and total rodents (TR; sum of all rodents trapped) were determined for each trapping site. Vegetation structural complexity for each spring/fall trapping site was indexed as tree density + shrub cover + deadfall and slash cover + graminoid cover. Each structural feature was ranked from 0 to 3, with 0 indicating the feature was absent and 3 indicating the feature was abundant with respect to other trapping sites. We used the Spearman rank correlation to determine the association between rodent capture rates and vegetation structural complexity for the 11 spring/fall trapping sites. Student's *t*-tests were used to detect differences

in capture rates between trapping sites for deer mice, red-backed voles, and total rodents at the $P < 0.10$ level.

Results

During the 1990-91 and 1991-92 field seasons, 7 martens in the Upper Big Hole study area were followed resulting in 197 locations. In the West Yellowstone study area in 1991-92 120 locations were collected from 5 martens. Habitats used by martens in each study area (Table 1) had higher numbers of trees, greater percentage of grass cover, and a lower percentage of non-vegetated cover than sites at random locations. Percentage of DWM coverage at the sites used by martens in the West Yellowstone study area was greater than that found at random locations.

Table 1. Structural characteristics of marten (M) and random (R) locations during the winters of 1990-91 and 1991-92 in the Upper Big Hole (n = 197) and West Yellowstone (n = 120) study areas of southwest Montana. Underlined values indicate significant differences from random points at P < 0.10. Values in parentheses are standard deviations. NA = data not available.

							Percent cover					
	# of trees		# of DWM[a] intercepts		DWM		Shrub		Grass		Non-vegetated	
Study area and year	M	R	M	R	M	R	M	R	M	R	M	R
Big Hole												
1990-91	6.4	5.0	4.9	5.7	NA		NA		NA		NA	
	(8.8)	(7.4)	(4.0)	(3.5)								
1991-92	7.0	5.9	5.2	5.6	19	19	34	41	38	19	25	34
	(3.2)	(2.8)	(3.2)	(3.2)	(12)	(11)	(21)	(23)	(17)	(16)	(18)	(19)
W. Yellowstone												
1991-92	5.2	3.4	2.9	2.7	27	15	23	18	32	23	23	45
	(2.6)	(1.6)	(2.0)	(1.8)	(17)	(8)	(20)	(12)	(14)	(13)	(17)	(25)

[a] DWM = downed woody material.

Table 2. Abundance rankings, structural diversity indices (Str. div., sum of abundance rankings, maximum of 12), and mean rodent capture rates for 11 spring/fall small mammal trapping sites in southwestern Montana. Ground cover, tree density, shrub and downfall cover were ranked on a scale from 0-3. Zero indicates the feature was absent, 3 indicates the feature was abundant with respect to other trapping sites. TN = trap nights, DM = deer mice, RBV = red-backed voles, TR = total rodents.

	Abundance rankings					Rodent captures per 100 TN		
Habitat type	Ground cover	Tree cover	Shrub cover	Downfall cover	Str. div.	DM	RBV	TR
Habitats used by martens								
Mesic subalpine fir	3	2	1	3	9	0.9	4.5	6.5
Xeric subalpine fir	3	3	1	3	10	1.0	2.6	7.0
Douglas-fir	2	3	1	3	9	3.9	10.6	14.5
Lodgepole pine/ graminoids	2	3	0	2	7	3.3	3.3	8.7
Habitats not used by martens								
Lodgepole pine	2	3	1	2	8	1.8	0.8	3.4
Clearcut	2	0	1	0	3	0.8	0	5.0
Lodgepole pine/ bitterbrush	1	2	2	1	6	4.8	0.2	7.3
Lodgepole pine/ sedge	2	1	0	1	4	0.7	0	2.9
Lodgepole pine/ kinnikinnick	2	3	0	3	8	5.6	0.8	7.5
Willow	2	1	0	1	4	0.7	0.7	6.0
Clearcut	2	0	2	2	6	10.0	0	13.3

Red-backed vole capture rates in spring and fall were strongly associated with high structural complexity (Spearman rank correlation = 0.83, $P < 0.01$) whereas deer mouse (Spearman rank correlation = 0.33, $P = 0.32$) and total rodent numbers (Spearman rank correlation = 0.39, $P = 0.23$) were not (Table 2). When capture rates of red-backed voles, deer mice and total rodents were compared to individual habitat variables, red-backed voles were correlated with tree cover (Spearman rank correlation = 0.78, $P < 0.01$) and downfall cover (Spearman rank correlation = 0.78, $P < 0.01$). Capture rates for voles at trapping sites located in habitat types used by radio-collared marten during winter were higher ($t = 3.66$, $P < 0.01$) than those at sites not used by martens. Capture rates for total rodents and deer mice did not differ ($t = 1.21$ and 0.64, respectively; $P > 0.25$) between habitat types used and not used by martens.

Capture rates for red-backed voles ($t = 3.44$, $P = 0.01$) and total rodents ($t = 2.77$, $P = 0.03$) in summer were higher in tree cover types used by martens in winter in the Upper Big Hole study area (Table 3). When capture rates of red-backed voles and deer mice were compared within selected cover types no differences were detected ($t = 0.47$, $P > 0.5$). Survival of deer mice and red-backed voles did not differ over summer ($t = 0.69$, $P = 0.50$), but voles showed higher recruitment rates ($t = 2.15$, $P < 0.10$) in selected cover types. Highest deer mouse and red-backed vole biomass losses occurred in trapping grids located in 4 habitat types favored by martens in winter in the 2 study areas (Table 3). Red-backed vole losses in habitats used by martens were nearly 6 times greater than red-backed vole biomass lost in unused habitats. When red-backed vole biomass losses were compared to those of deer mice, red-backed vole losses were 2 times greater in habitats used by martens.

Discussion

Red-backed vole densities appear to better determine the use of complex habitats by martens than do the densities of deer mice or total rodents. Three consecutive years of research on the ecology of the marten in southwest Montana (Fager 1991, Kujala 1993, Coffin 1994) showed that martens used habitats with high structural complexity. These structurally complex habitats were characterized by a high number of downed and dead woody material ≥7.6 cm, high basal area, and mesic sites that supported more grass cover than that found at randomly placed plots. Red-backed vole capture rates were significantly higher in these types of habitats during the spring, fall and summer trapping periods, than in less complex habitat types. Furthermore, red-backed vole capture rates showed a strong correlation with high structural diversity, whereas those of deer mice and total rodents did not. Captures of red-backed voles also correlated well with downed woody cover. Although the overall structure of the habitat is important,

Table 3. Mean captures per 100 trap nights (TN), survival, recruitment and biomass lost (grams) for deer mice (DM), red-backed voles (RBV), and total rodents (TR). Data are for 8 100 × 100-m trapping grids (100 traps/grid) in southwest Montana during the summers (July to September) of 1991 and 1992. NA = data not available.

Habitat type	Captures/100TN			Survival and recruitment				Biomass lost	
				DM		RBV			
	DM	RBV	TR	Surv	Recr	Surv	Recr	DM	RBV
Habitats used by martens									
Spruce	9.7	5.8	16.5	0.72	0.41	0.69	0.57	88	49
Subalpine fir	0.5	7.0	10.7	NA	0	0.31	0.71	0	226
Douglas fir	7.2	17.8	26.3	0.69	0.45	0.59	0.61	97	344
Lodgepole pine/graminoids	8.0	2.2	13.5	0.54	0.63	0.63	0.62	135	29
Habitats not used by martens									
Lodgepole pine/duff	8.3	1.3	5.8	0.17	0.64	0	0.50	56	46
Clearcut	1.5	0	7.3	0	1.0	NA	0	42	NA
Lodgepole pine/kinnikinnick	5.7	2.3	13.0	0.62	0.34	0.17	0.75	104	44
Lodgepole pine/bitterbrush	1.3	3.7	11.3	0	1.0	0.35	0.79	41	20

downed woody material is probably the key component. Martens exploited small mammals in our study by utilizing an array of subnivean access sites that put them in greater contact with voles than with other rodents at a given site, thus making voles more available to martens in these areas.

We assume that winter is the most critical time for marten. We could not sample one of the major components of the winter prey base directly, so we used small mammal data from spring, fall and summer as an estimate of this prey base. Total rodent captures or prey density estimates during these times of the year

may include other species, such as chipmunks (*Tamias* spp.), golden-mantled ground squirrels (*Spermophilus lateralis*) or western jumping mice (*Zapus princeps*). These species hibernate and are not readily available to marten during the winter months. Although deer mouse (Fairbairn 1977) and red-backed vole (Merritt and Merritt 1978) populations decline during winter, they are still active and available to martens throughout the winter. Because small mammal trapping was done during the spring, summer, and fall, total rodent capture rates or simple prey density may be misleading regarding availability of prey during winter. Species-specific availability of prey, knowledge of prey population dynamics, and site structure should be considered.

Prey density is an important component of food dependability to martens (Weckwerth and Hawley 1962, Thompson and Colgan 1987), but prey vulnerability may be just as important. Red-backed vole biomass losses far exceeded those of deer mice, but capture rates between the 2 did not differ in selected habitat types. Thus, equal densities of small mammals such as deer mice and red-backed voles do not mean equal productivity. Voles are short-lived. Therefore, a low density of red-backed voles may be deceptive. Martens use a large area, so even a low density of very vulnerable prey might be sufficient to support them. Red-backed voles have a higher reproductive capacity and are therefore more abundant making them more available to marten. We conclude that red-backed voles are more vulnerable to predation in more structurally complex habitats not only because marten have access to the subnivean space via downfall or tree boles, but because red-backed voles also prefer these more complex habitats for food and cover.

Conclusion

Measuring small mammal populations in general, or in downfall in particular, is not a complete estimate of the value of a site to martens. Our results support the hypothesis that martens select habitats in our study areas based on the availability and density of vulnerable red-backed voles, rather than just the density of small prey mammals or habitat structure. Summer or spring and fall estimates may or may not be valid as estimates of winter prey levels. Accurate winter estimates are difficult, if not impossible, to obtain and most researchers will be forced to rely on estimates from other seasons if they want estimates of prey availability. Both density estimates and "change in number over winter,, estimates will give a poor idea of marten-prey relationships unless species composition and population dynamics of rodents are considered. Maintaining structurally complex forests will provide martens with foraging and resting sites, as well as food and cover for prey species.

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RELATIONS AMONG FISHERS, SNOW, AND MARTENS IN CALIFORNIA: RESULTS FROM SMALL-SCALE SPATIAL COMPARISONS

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Abstract: A recent publication hypothesized that deep snowfall can limit fisher (*Martes pennanti*) populations, and high fisher populations limit marten populations (*M. americana*). These hypotheses were evaluated by comparing the historic (1919-1924) and current (1989-1994) distributions of both *Martes* species in California to current snowfall distributions and forest types presumed to be habitats for each species. Data on historic distributions of fishers and martens came from the locations of trapped animals reported by Grinnell et al. (1937), whereas current distributions came from detection surveys (sets of track-plates, cameras, and both) conducted primarily by personnel of the US Department of Agriculture (USDA) Forest Service. Information on forest types came from a computerized database created by the USDA Forest Service from satellite imagery. In both time periods, areas occupied predominantly by martens were closely associated with forested areas with the deepest snow (>23 cm per winter month), areas occupied predominantly by fishers were forested areas with low monthly snowfall (<13 cm), and overlap zones with both species were in forested areas of intermediate monthly snowfalls (≥13 to 23 cm). In contrast, there was poor spatial correspondence in both time periods between the occurrences of fishers and martens and the small-scale distributions of forest types. Although we continue to recognize the importance of forest structure and prey populations on the distribution of both species of *Martes*, these findings suggest that climatic and interspecific factors deserve more attention as factors potentially affecting fishers and martens.

Introduction

Based on a review of North American literature and an evaluation of the distributions of fishers (*Martes pennanti*) and martens (*M. americana*) harvested in Maine, Krohn et al. (1995) proposed that (1) fisher populations can be limited by deep snow, and (2) high fisher populations limit marten populations. These 2 hypotheses were evaluated by assessing variation across 3 regions of Maine (i.e., predominately martens in the north, a central area of overlap, predominately fishers in the south) in the age ratios of fishers and martens taken by fur trappers from 1980 to 1984. The mean number of immatures per adult fisher decreased from south to north as snowfall amounts and frequencies increased, which is consistent with the hypothesis that deep snows limit fishers (i.e., deep snow is stressful and lowers reproductive success). Age ratios of martens increased beyond their biological potential with increased densities of harvested fishers (and numbers of martens harvested decreased drastically), suggesting that most martens within predominantly fisher habitat are dispersing juveniles. Thus, patterns in marten age ratios were consistent with the hypothesis that high populations of fishers limit martens. However, Krohn et al. (1995) recognized that association does not prove causation, nor were they sure that harvested animals represented population distributions.

The purpose of this study was to assess the above 2 hypotheses with data on the distribution of fishers and martens in California. Unlike Krohn et al.'s (1995) evaluation that relied on harvested animals, California has been closed to fur-trapping for fishers since 1945-46 (Lewis and Zielinski 1996) and since 1953-1954 for martens (Kucera et al. 1995). Thus, this analysis was based, in part, on non-fatal surveys specifically established to detect fishers and martens. Although fishers, and presumably martens, are caught in traps set for other carnivores (Lewis and Zielinski 1996), the lack of legal fur-trapping for *Martes* in California means that natural environmental conditions, not direct mortality from humans, probably drive the current statewide distributions of both species. In addition to assessing current distributions, we examined the historic distributions of fishers and martens in California by plotting the harvest records reported by Grinnell et al. (1937). The historic and current datasets encompassed enough environmental variation to make meaningful comparisons of factors hypothesized to affect fisher and marten distributions over large areas (i.e., small-scale).

Data Sources and Study Predictions

Historic Distribution

Harvest data for fishers and martens between 1919 and 1924 were taken from Grinnell et al. (1937). Specifically, we used a copy machine to enlarge figures 67

(marten harvest) and 75 (fisher harvest) from Grinnell et al. (1937) and entered the 153 points (fishers = 75; martens = 78, excluding the Humboldt subspecies) representing harvested animals into ARC/INFO (Environmental Systems Research Institute, Redlands, California; use of commercial names does not imply endorsement by the US Government). Fisher points were assumed to be individual animals whereas the points of harvested martens were coded as ≤5 martens or >5 martens as indicated by Grinnell et al. (1937).

Current Distribution

The distribution of fishers and martens for the period 1989-1994 was determined from the results of field surveys conducted throughout these species' historic ranges in northern and central California (Zielinski et al., this volume). Most of the surveys were conducted by USDA Forest Service personnel, or contractors, on National Forest lands using enclosed track plates or line-triggered cameras (Zielinski 1991). However, the sample also included a significant number of surveys on state and private forested land. Each of the 217 surveys consisted of multiple stations (mean ± SD = 18.3 ± 13.2) distributed at about 1-km intervals along forest roads and checked every 12.6 ± 3.9 days. Almost all surveys were conducted during the snow-free season (May through October). Most surveys were initiated by biologists interested in determining whether either marten or fisher occurred in an area scheduled for timber harvest (Zielinski et al., this volume). Thus, these surveys do not represent a formal sampling design.

Successful surveys (n = 85) were defined as those surveys where 1 or more *Martes* were detected; unsuccessful surveys (n = 132) were those where no fishers or martens were detected. Adjacent surveys may be dependent in the sense that an individual animal could have visited more than 1. Because martens have smaller territories (Katnik 1992) and dispersal distances (Phillips 1994) than fishers (Arthur et al. 1989, 1993), dependent surveys could be more of a problem with fishers than martens. To allow readers to judge the independence of individual surveys, the scaled diameters of dots representing all surveys in this paper are ≈15 km in diameter. This compares to a mean maximum dispersal distance for juvenile fishers of 16.4 ± 4.5 km (Arthur et al. 1993).

We excluded the Humboldt marten (*M. a. humboldtensis*) from our spatial analyses because only sparse historic data exist (Grinnell et al. 1937), and the subspecies is now extremely rare or extinct (Kucera et al. 1995). However, we included this subspecies in our discussion of factors potentially affecting the distributions of *Martes* in California.

Snowfall Data

Monthly mean snowfall data for California were obtained from the National Climatic Data Center, National Oceanic and Atmospheric Administration (NOAA),

in Asheville, North Carolina. Data for 1915-16 through 1925-26 were available from too few stations ($n = 17$) to allow us to plot the distribution of snowfall for this period. Therefore, we had to compare the historic distributions of *Martes* to current snowfall patterns. Current snowfall data covered the winter of 1982-83 through 1991-92. This period was presumed to be long enough to have affected current *Martes* populations, should such relations exist, and recent enough to coincide with the years most surveys were run. Spatial distribution of snowfalls was characterized for each weather station using the amount of snowfall per month from December through March. Weather stations with fewer than 8 years of data over the 10 years of interest were excluded from our analyses. Out of a total of 463 weather stations statewide, 390 had usable data. Contours of mean monthly snowfalls calculated from the 390 stations were made using the software package SURFER Version 4 (Golden Software, Golden, Colorado). SURFER will interpolate a grid of ≤255 cells, so the north-south dimension of California was interpolated using 255 cells (each ≈ 4.1 km/side) with 200 cells spanning east-west. An inverse distance weighting was used to calculate grid values. The snowfall grid was imported into ARC/INFO and printed.

To compare the locations and sizes of snowfall regions to the distributions of fishers and martens, we calculated means and standard deviations of mean monthly snowfalls (cm), 1982-1991, corresponding to the locations of *Martes* in both the historic and current datasets. Statistics were calculated for sites with only fishers (8.1 ± 12.7; $n = 121$), both species (17.8 ± 18.7; $n = 11$), and only martens (27.6 ± 23.1; $n = 106$). The midpoints between fishers and both species (13 cm), and between both species and martens only (23 cm), defined snowfall regions that were then overlaid onto the *Martes* distribution data. If the fisher/snow and fisher/marten hypotheses function as proposed (Krohn et al., 1995), then the small-scale distributions of both species should coincide with the snowfall zones defined by these mid-points (i.e., <13 cm: mostly fishers; 13-23 cm: overlap of 2 species; >23 cm: mostly martens).

Forest Types

We also looked at the current and historic distributions of the 2 *Martes* species in relation to forest types, as defined and mapped in 1979 by the California Vegetation Map (CALVEG) (Matyas and Parker 1980). The CALVEG forest types were mapped at 1:250,000 scale by visual inspection of color infra-red satellite imagery with results being verified from current soil-vegetation maps and by field checking approximately 8052 km (Matyas and Parker 1980). Mapped forest types were assigned as used by fishers or martens based on personal experience (WJZ) and a review of studies done in California (Table 1). We compared the species' distributions, as measured by successful surveys, to the distributions of habitats used by fishers, martens, and both species. Because of a

Table 1. Fisher and marten habitats based on forest-type associations observed and reported[a]. Forest types as defined by the California Vegetation Map (Matyas and Parker 1980).

Fisher[b]	Marten[c]
Douglas fir-tanoak-madrone	Lodgepole pine
Douglas fir-pine-madrone	Mixed conifer-fir[d]
Jeffrey pine	Mountain hemlock
Tanoak-madrone	Redwood-Douglas fir[d]
Madrone-black oak	Red fir
Mixed conifer-fir[d]	White fir[d]
Mixed conifer-pine	
Oregon white oak	
Ponderosa pine	
Redwood-Douglas fir[d]	
White fir[d]	

[a] Includes observations made by W. J. Zielinski on fishers in northwestern California and the southern Sierra Nevada Mountains, and on martens in the southern and northern Sierra Nevadas.

[b] Schempf and White (1977), Buck (1982), and Self and Kerns (1992).

[c] Schempf and White (1977), Simon (1980), Zielinski (1981), Spencer et al. (1983), Hargis and McCullough (1984), Martin (1987), and Self and Kerns (1992).

[d] Forest types used by both species.

lack of historic forest type data, distributions of fishers and martens for 1919-1924 had to be compared to current distributions of forest types. Because major vegetation types were mapped at a small scale, and types are strongly associated with landforms such as deserts and mountains (Matyas and Parker 1980), we believe CALVEG to be a reasonable small-scale representation of forest types.

Study Predictions and Statistical Analyses

If snow limits fisher populations in California, then fishers should mostly occur in those forested portions of the state where snowfall is low to moderate (<13 cm per winter month; see Snowfall Data, above, for rationale). If fishers occur in areas of deep snowfall, these areas would be expected to be largely covered with closed-canopy, coniferous forests that alter the structure of snow accumulating on the ground. Areas where both species occur should be in transitions

between deep and low snowfalls (13-23 cm), or between open and closed-canopy forests where snow amounts are high and similar. If high fisher populations limit martens, then high marten populations will coincide with areas without fishers or with low densities of fishers, specifically in an area or areas of deep snow (>23 cm).

The mean monthly amounts of snowfall at sites with fishers and martens were compared with *t*-tests. Specifically, we tested for equality of group means between species, in both the historic and current data, without assuming equal variances (Zar 1984). Chi-square tests were used to compare, in both datasets, the distribution of each species by snowfall categories presumed to represent 3 degrees of suitability (as defined above in Snowfall Data). Similarly, chi-square tests were also used to evaluate the distribution of both *Martes* species relative to forest types (as defined in Table 1) presumed to be suitable *versus* unsuitable habitats.

Results

Martes Distributions

The historic distribution of martens consisted of a large, central core corresponding to the locations of the Sierra Nevada Mountains (Fig. 1B). In the north, there was a small zone of overlap; in the south, the Marten Core graded into an elongated zone with both species (Fig. 1B). Note that if *M. a. humboldtensis* were included (Fig. 1A), the western edge of Group A (Fisher North: Fig. 1B) would have included martens. Areas where fishers predominated were located at the northwest and southwest ends of the 2 overlap areas (Fig. 1B).

Because successful and unsuccessful surveys were roughly distributed the same (Fig. 2A), we deleted unsuccessful surveys from the determination of the current distributions. In ignoring unsuccessful surveys, we assumed that they represent either no fishers or martens, or a *Martes* population similar in composition to adjacent successful surveys. We believe that successful surveys are an unbiased small-scale representation of the current distributions of fishers and martens in California, excepting the east side of the southern Sierras that was poorly sampled (Fig. 2B) and possibly the western side of the central Sierras that had few successful surveys (Fig. 2A). Again, current survey data show a large area occupied by martens along the Sierra Nevadas that grades both north and south into overlap zones, and then into 2 areas occupied mostly by fishers (Fig. 2B). In terms of the composition of the surveys that made up the 5 spatial groups, Fisher North consisted of 29 surveys, 28 with only fishers and 1 with both species; Overlap North included 4 surveys, 3 with both species and 1 with martens only; the Marten Core had 23 marten-only surveys; Overlap South had 12 surveys, 6 with both species, 3 with fishers only, and 3 with martens only; and Fisher South consisted of 17 surveys: 15 with only fishers, 1 with martens only, and 1 with both species.

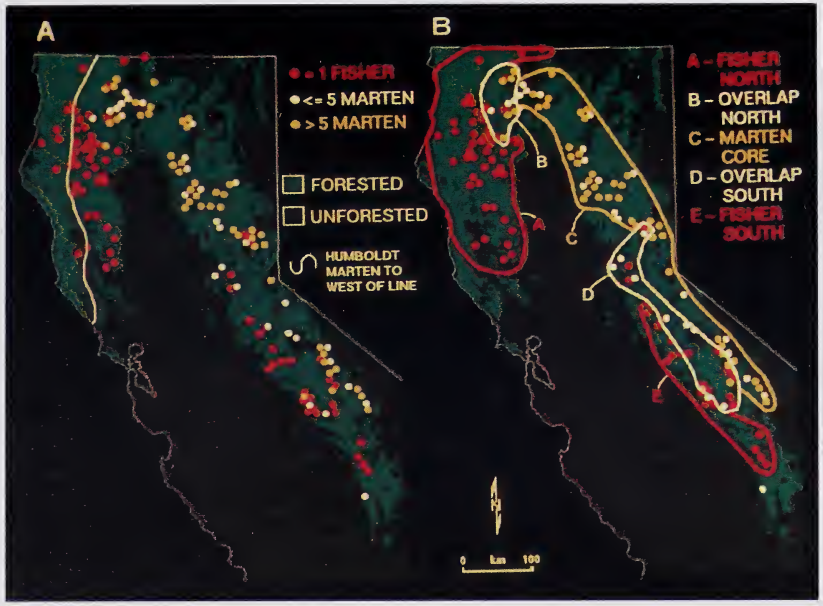

Figure 1. Distributions of forested lands, and fishers (*Martes pennanti*) and martens (*M. americana*) in California as indicated by the harvest records in Grinnell et al. (1937) for 1919-1924 (A). Spatial groupings of *Martes* (excluding the Humboldt marten, *M. a. humboldtensis*, which went extinct) are shown in B. Data on forest coverage from California Vegetation Map (Matyas and Parker 1980).

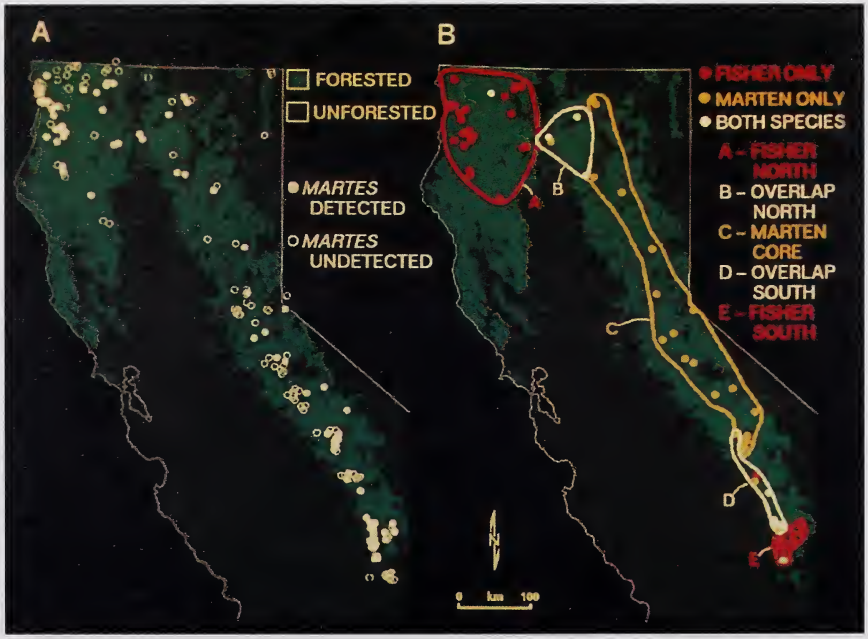

Figure 2. Distribution of forested lands and *Martes* surveys (A), and species groupings from surveys where *Martes* were detected (B) in central and northern California, 1989-1994. Data on forest coverage from California Vegetation Map (Matyas and Parker 1980).

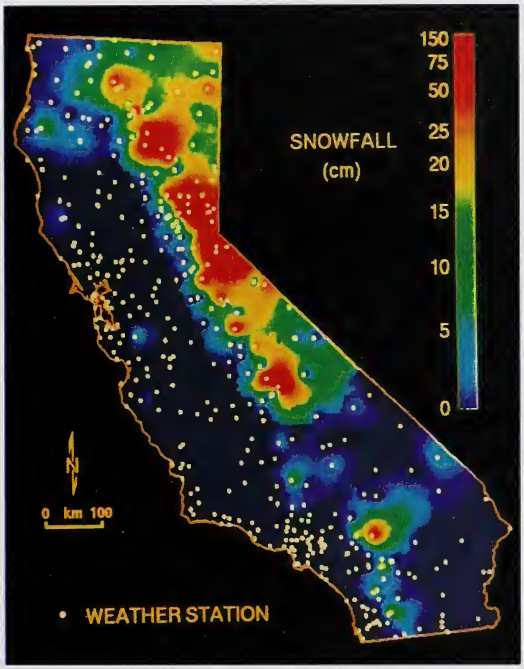

Figure 3. Contours of mean monthly snowfall (in centimeters) for California, based upon means from December to March, 1982-83 to 1991-92. Contours begin at 1.0 cm and are separated by 9.0 cm increments, with the maximum mean monthly snowfall recorded being 173 cm. Based on 390 weather stations with ≥8 years of data.

Snowfall Distribution

Weather stations were widely distributed across California (Fig. 3), with each station representing an average of 1039 km^2. The mean amount of snow falling per winter month varied greatly, with the highest amounts in the northern Sierra Nevada Mountains, and in the southern Cascade Mountains in north-central California (Fig. 3). Because the current distribution of snowfall was closely associated with mountainous areas, and mountains were stable over the time interval of interest, we believe these data represent the approximate distribution of snowfall during the historic period, although we recognize that annual snowfall amounts and distributions are highly variable in California (NOAA records).

The distribution of martens, both in terms of historical data (Fig. 4A; excepting the Humboldt subspecies) and current surveys (Fig. 4B), corresponded closely to the regions of heaviest snowfall. According to current survey data, martens do not occur in the deep snow area in the southern Sierras (Fig. 4B). This area, however, was largely unsampled (Fig. 2). Personal observations (WJZ) and data in Schempf and White (1977) suggest that Group C in Figure 4B should extend to the southern tip of the Sierra Nevada Mountains, corresponding to the southernmost areas of monthly snowfall >23 cm (Fig. 4B). In contrast to martens, fishers occurred mostly in those forested areas with mean monthly snowfalls <13 cm (Fig. 4). Overlap zones occurred in areas of rapidly changing snowfall amounts (13-23 cm per month), specifically at both ends of the Sierra Nevada Mountains and along the western slope of the southern Sierras (Fig. 4). Fishers used areas with significantly ($P < 0.001$) less snowfall than martens in both time periods, but mean snowfall depths did not change ($P > 0.10$) within species between periods (Table 2). Furthermore, snowfall zones and *Martes* groups were spatially related ($P < 0.001$) during both time periods (Table 3). However, because boundaries of the *Martes* groups were hand drawn from non-random data that were incomplete, the spatial relations in Table 3 and Figure 4 are only approximations.

Table 2. Statistical comparisons of monthly snowfall depths (cm) at locations in California where fishers (*Martes pennanti*) and martens (*M. americana*) occurred based on historical harvest (except *M. a. humboldtensis*) and current survey data. Distribution data from Figures 1B and 2B were overlaid on Figure 3 to obtain mean (1982-1991) snowfall amounts for individual locations.

Monthly snowfall statistics	Historical data (1919-24)		Current data (1989-93)	
	fishers[a]	martens[b]	fishers[c]	martens[d]
Mean	10.5	25.9	6.9	28.3
Standard deviation	14.5	21.5	11.9	25.5
Range	0.2-62.6	1.8-116.2	0.6-66.6	1.3-108.3
Sample size	75	78	57	39

[a] *versus* [b] Significantly different; $t = 5.224$, df = 135.8, $P < 0.001$.
[c] *versus* [d] Significantly different; $t = -4.887$, df = 49.4, $P < 0.001$.
[a] *versus* [c] Not significantly different; $t = -1.597$, df = 129.2, $P = 0.12$.
[b] *versus* [d] Not significantly different; $t = 0.502$, df = 65.5, $P = 0.62$.

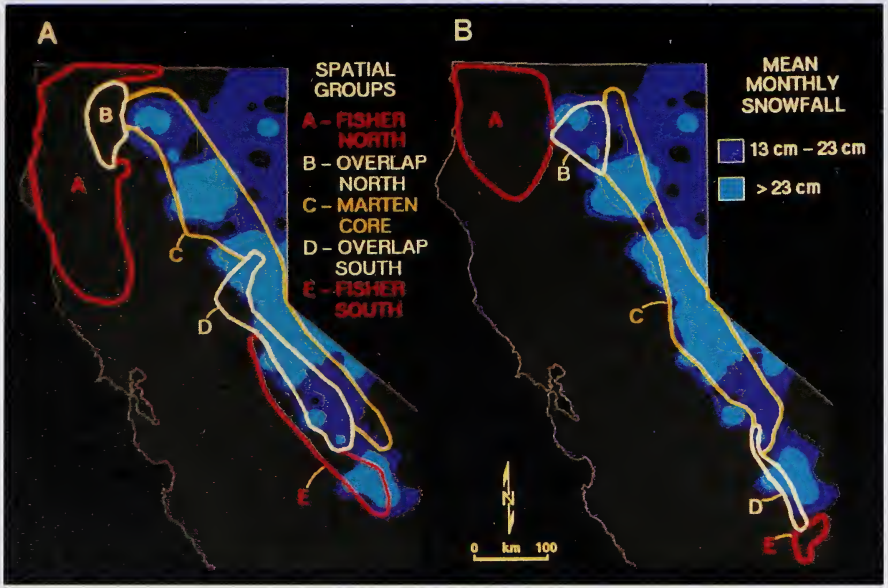

Figure 4. Relationship between the historical (A) and current (B) distributions of *Martes* in California (from Figs. 1, 2) and the current snowfall conditions (from Fig. 3).

Table 3. Proportions, and areas in 1000 km² in parentheses, of *Martes* spatial groups relative to snowfall zones.

Mean snowfall (cm) per winter month	Historical distribution[a]			Current distribution[b]		
	fishers	overlap	martens	fishers	overlap	martens
<13	0.88	0.42	0.14	0.99	0.16	0.07
	(36.2)	(6.95)	(4.41)	(21.22)	(1.16)	(1.90)
13 to 23	0.04	0.28	0.35	0.01	0.57	0.35
	(1.74)	(4.65)	(11.23)	(0.32)	(4.19)	(8.78)
>23	0.08	0.30	0.51	0.00	0.27	0.58
	(3.05)	(4.81)	(16.25)	(0.00)	(1.98)	(14.78)

[a] Areas calculated from Figure 4A. Snowfall and distribution significantly related; $\chi^2 = 41.2$, df = 2, $P < 0.001$.
[b] Areas calculated from Figure 4B. Snowfall and distribution significantly related; $\chi^2 = 44.9$, df = 2, $P < 0.001$.

Forest Types

Despite the presence of suitable habitat types in the southern Cascades and northern Sierra Nevadas (Fig. 5A), the historical view of fisher distributions (Grinnell et al. 1937) suggests that fishers may have been less common in these areas than elsewhere in California. Whether this distribution was the historic condition or reflects human effects on forests and fishers prior to their assessment is unknown. Habitat for the Humboldt marten was apparently available in the North Coast ranges in historic times (Fig. 5B), but today this subspecies is either at very low population density or extirpated (Kucera et al.1995; Fig. 2B).

Currently, fishers are at very low densities or absent from the southern Cascades through the central Sierra Nevada, despite the presence of apparently suitable habitat types (Fig. 6A). In addition, martens were detected by surveys as far north as the interior part of northern California where, according to forest types present, habitat should be unavailable for martens (Fig. 6B). We also note that no martens were detected in northwestern California, despite the occurrence of suitable habitat types (Fig. 6B) and the historic use of the west side of this area by the Humboldt marten (Fig. 1A).

Using the sizes of the spatial groups defined by the harvest and survey data as indices to occupied ranges, significantly more than half of the presumably suitable habitats for fishers ($P < 0.10$) and martens ($P < 0.01$) appeared unoccupied

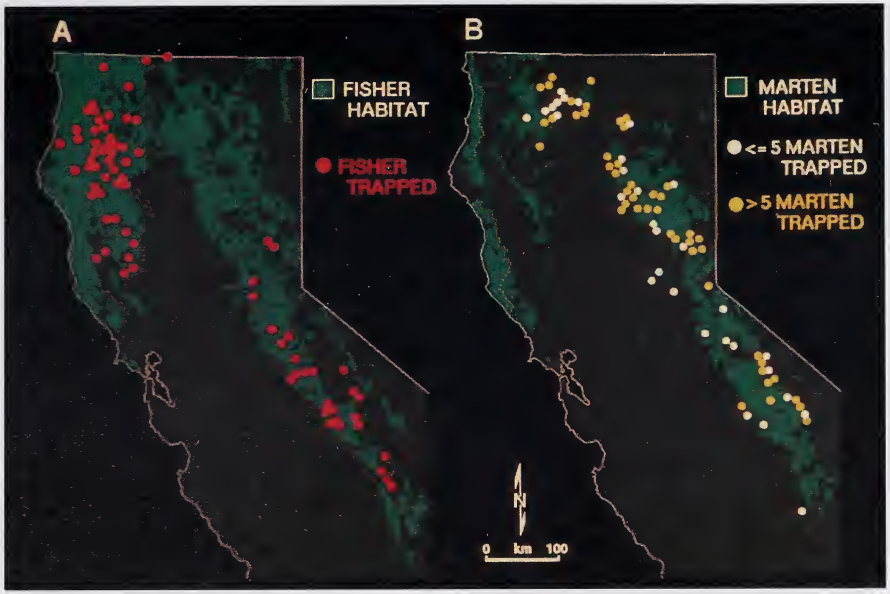

Figure 5. Spatial relations between historical harvest of fishers and martens and habitats used by fishers (A) and martens (B). Forest cover types are listed in Table 1, and are derived from California Vegetation Map (Matyas and Parker 1980).

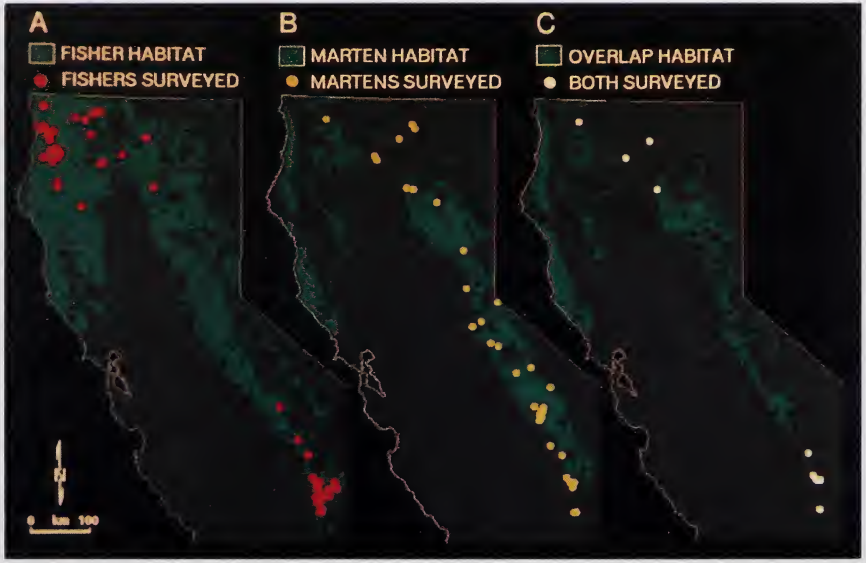

Figure 6. Spatial relations between current surveys of fishers and their habitats (A), martens and their habitats (B), and both *Martes* species and shared habitats (C). Forest cover types used by fishers, martens, or both are listed in Table 1, and are derived from California Vegetation Map (Matyas and Parker 1980).

Table 4. Proportions, and areas in 1000 km² in parentheses, of *Martes* spatial groups relative to forest types that are suitable habitats for fishers, martens, and both species.

Suitable habitats[a]	Historical distribution[b]			Current distribution[c]		
	fishers	overlap	martens	fishers	overlap	martens
Occupied by spatial group(s)	0.44 (22.10)	0.16 (3.91)	0.39 (5.28)	0.27 (13.45)	0.02 (0.46)	0.48 (6.44)
Unoccupied by spatial group(s)	0.56 (28.62)	0.84 (20.78)	0.61 (8.11)	0.73 (37.26)	0.98 (24.24)	0.52 (6.96)

[a] Forest types documented to have been used in California by fishers, martens, or both species (Table 1).

[b] Areas calculated from an overlay of spatial groups in Figure 1B on presumably suitable habitats in Figure 6. Significantly more habitat unoccupied than occupied; $\chi^2 = 5.72$, df = 2, $P < 0.10$.

[c] Areas calculated from an overlay of spatial groups in Figure 2B on presumably suitable habitats in Figure 6. Significantly more habitat unoccupied than occupied; $\chi^2 = 11.37$, df = 2, $P < 0.01$.

during both time periods (Table 4). Overall, small-scale maps of forest types known to be used by fishers and martens in California were poor predictors of the occurrence for both species (Figs. 5, 6).

Discussion

Grinnell et al. (1937:25) stated that fishers ranged ". . . south from Mount Shasta and Lassen Peak throughout the main Sierra Nevada to Greenhorn Mountain, in north central Kern County." Although the map of fisher distribution in Grinnell et al. (1937), on which our Figure 1A is based, gives the impression that fishers may have been less common in the southern Cascades, northern Sierra Nevadas, and east side of the southern Sierra Nevada, than in the rest of their range, these results must be interpreted with caution. Figure 1 is based on only 1 5-year period, prior to which there was already concern that trapping had decreased the population of fisher in California to a point where season closings were recommended (Dixon 1925, Grinnell et al. 1937). In terms of current distribution patterns, if the west side of the central Sierras was under-sampled, and fishers were more common here than suggested by Figure 2, then the boundaries of Overlap South and Fisher South could be similar to the historic pattern (Fig. 1B).

Because neither the historic nor the current data on *Martes* distributions were based on uniform sampling effort (or even known effort in the case of the historical data), we did not assess temporal changes in the distribution of *Martes*. Furthermore, boundaries of the various spatial groups may be wrong, as specifically noted above for the current occurrence of martens on the east side of the southern Sierras. However, even though both distribution datasets probably do contain errors caused by over- and under-sampling, we believe that both datasets do provide an adequate small-scale representation of the major distribution patterns of *Martes* in California.

Fisher/Snow Hypothesis

In the historical and current data on distributions, fishers were clearly associated with areas of low snowfall across a wide range of forest types. Furthermore, forest types known to be used by fishers in California appeared to be used less when located in deep snow areas. Forested areas inhabited by both fishers and martens occurred in areas of intermediate snowfall, across a wide range of forest types, and in topographic breaks where snowfall amounts changed greatly over a small area. These patterns are consistent with the hypothesis that deep snow can limit fisher populations.

A logical question is how can snow, which restricts the travel of fishers for less than 4 months out of a year, determine the year-long distribution? Krohn et al. (1995) proposed an ultimate mechanism based on energetics and fitness. A more proximate mechanism could involve the animal's dispersal and spacing patterns. Because most juvenile fishers disperse during the snow season (Arthur et al. 1993), and because adult females seem to have territories that are more or less fixed for life (Arthur et al. 1989), the initial selection of the home range may exclude deep snow where travel is impaired. Although some adult males shift territory locations after the spring breeding season (Arthur et al. 1989), it is unlikely that, even if unimpaired by snow, males would establish a territory in an area devoid of resident females. Of course, because energetic balance varies not only with snow conditions (i.e., depth, frequency, hardness), but also with such factors as prey abundance and availability, we suspect that there is no absolute line between suitable and unsuitable habitats, but instead an ever-shifting zone of varying degrees of suitability relating to energy inputs versus outputs.

Fisher/Marten Hypothesis

Were martens present during both time periods in the northern Sierras and southern Cascades because of low fisher populations, presence of deep snow, or other factors? Because we have no data directly bearing on fisher/marten interactions or other possible factors, we cannot answer this question. It appears that the martens inhabiting the coastal forests of northwestern California in the early

1900s did not persist (Schempf and White 1977; Kucera et al. 1995), probably due to the rapid loss of original redwood forest habitat in the region at the turn of the century (Fox 1989, Buskirk and Ruggiero 1994). Fishers have never been common in the redwood forest along the coast (Grinnell et al. 1937; Zielinski et al. 1995), but competition with fishers may also have contributed to the decline in the Humboldt marten. Studies of large numbers of radio-collared fishers and martens living sympatrically are needed to clarify an issue that has been the subject of comment in the technical literature throughout North America for almost nine decades (Table 5).

Alternative Hypotheses

Although the above findings are consistent with the 2 hypotheses of interest, we recognize that other factors affect the distributions of both *Martes* species. For example, CALVEG did not include information on the current developmental stage and timber harvest history of each polygon, nor was the suitability of landscapes surrounding survey locations assessed (e.g., Rosenberg and Raphael 1986). Statewide data on these features will rarely, if ever, be available for the historical period. Moreover, there are other sources of information on the distribution of vegetation in California (e.g., Griffin and Critchfield 1976, Airola 1988) that in some cases disagree with CALVEG (e.g., in the north-central area where CALVEG has no suitable marten habitat). Thus, the lack of agreement between forest types and *Martes* distributions may be because snow is a better explanatory variable, or because the CALVEG data excluded important habitat variables.

In a review of the habitat ecology of fishers and martens, Buskirk and Powell (1994) argued that habitat structure is important to both species. Although these authors did not specify the kind of structure needed, Powell and Zielinski (1994:53) stated that ". . . vertical and horizontal complexity created by a diversity of tree sizes and shapes, light gaps, dead and downed wood, and layers of overhead cover. . ." are important to fishers. Similarly, Buskirk and Ruggiero (1994) emphasized the importance of forest structure, including coarse woody debris and large-diameter trees, to martens. Unfortunately, the available habitat data lacked subcanopy structural characteristics.

Approximately 8 fishers were reportedly taken within the range of the now-extinct Humboldt marten between 1919 and 1924 (Fig. 1A). During this same 5-year period, 43 Humboldt martens were trapped (Grinnell et al. 1937). The low number of fishers relative to martens is consistent with the hypothesis that high fisher populations can limit martens. However, because this area currently receives little snowfall (Fig. 3), and probably did so historically, the low fisher population in this area is inconsistent with the notion that deep snow limits fishers. However, we have no basis to argue that snowfall is the only factor that can limit fisher populations. We note that there are other areas in California where snowfall

Table 5. Literature comments on the interaction between fishers (*Martes pennanti*) and martens (*M. americana*).

Location	Comments	Citation
Maine	Noted an apparent inverse pattern between the numbers of fishers and martens trapped.	Hardy (1907)
California	Cited an experienced trapper who believed that fishers preyed upon martens, but found ". . . little first-hand confirmation. . ." Cited a letter stating that "Old hunters say they [martens] will not live where there are fishers."	Grinnell et al. (1937:200, 210)
Ontario	Reported an inverse relation between fisher and marten harvests, but noted enough exceptions to reject the idea that ". . . one species might suppress the level of the other."	de Vos (1952:29)
New Hampshire	Documented instances of fishers killing martens in traps, and stated that ". . .there is some evidence that fisher also prey on marten . . ." and cited Piper who felt that ". . .fisher are partially responsible for the depletion of marten in the White Mountains National Forest."	Silver (1957:262)
Ontario	Reported marten remains in the stomach of a fisher. Apparently the fisher came from an area open to fur-trapping, so the marten(s) may have been trapped.	Daniel (1960)
Ontario	Believed that fishers and martens competed for den sites and food.	Clem (1977)
Manitoba	Reported 2 cases, in an area without fur trapping, of martens eaten by fishers.	Raine (1981)
Ontario	An inverse relation (see de Vos 1952) noted between fisher and marten harvests. Acknowledged the possibility of ". . .a fisher-marten interaction. . ."	Douglas and Strickland (1987:519)

Table 5. Continued.

Location	Comments	Citation
Maine	Reported an inverse relation between the statewide harvests of fishers and martens, 1980-1987. Formally proposed that high fisher populations could limit marten populations.	Krohn et al. (1995)
Maine	Of 13 radio-collared martens killed by predators in north-central Maine, 3 were attributed to fishers, 6 to other known predators, and 4 to unknown predators.	Hodgman et al. (this volume)

is low and forest types typically used by fishers occur, and yet fishers are seemingly absent today. Specifically, the west side of the central and northern Sierra Nevada Mountains apparently do not now support fishers. It's possible that mining and timber harvesting in the Sierras reduced habitat quality, possibly through fragmentation and the reduction of structural diversity.

California-Maine Comparison

Krohn et al. (1995) proposed that in regions with more mountainous terrain than Maine, transitions between fisher and marten areas (i.e., overlap zones) would occur over shorter distances. Clearly, overlap zones were smaller and more distinct in California (for both time periods) than Maine. In addition, differences in the distributions of the 2 *Martes* species in Maine were subtle, being largely based on differences in density, whereas in California spatial groups were classified solely by species composition. In Maine the 48-cm snowfall contour (mean monthly, December to March) corresponds to the center of overlap between the distribution of the 2 *Martes* species (Krohn et al. 1995), whereas data for California suggest a threshold around 18 cm (see Snowfall Data in Methods). We speculate that the more open coniferous forests of California have less effect on snow structure than the more closed-canopy coniferous forests of Maine, and thus the level at which mean monthly snowfall affects fishers is lower in California than Maine. However, snowfall frequencies and snow structure (i.e., crusting conditions), which could also affect the mobility of fishers and martens (Raine 1981), probably also differed between the 2 states.

Conclusions

The small-scale analyses reported here do not prove that deep snows limit fishers, nor that high fisher populations limit martens. With the exception of the now-extinct Humboldt marten, however, both hypotheses explain the *Martes* distribution patterns in 2 California datasets. Thus, we encourage others to consider the ramifications of these 2 hypotheses and to carefully design and conduct tests of the 2 relations proposed by Krohn et al. (1995).

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HOME-RANGE AND HABITAT USE BY FISHERS TRANSLOCATED TO THE ASPEN PARKLAND OF ALBERTA

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Abstract: The home-range characteristics and seasonal habitat preferences of 16 (6 males and 10 females) radio-collared fishers (*Martes pennanti*), which had been translocated to the aspen parkland region of central Alberta, were studied from March 14, 1990 to September 15, 1992. Mean annual home-range areas were 24.3 (SE = 11.1) km^2 for males, and 14.9 (± 3.5) km^2 for females. Home-range sizes for both sexes were reduced during cold weather, averaging 14.5 (± 3.1) km^2 when the ambient air temperature was above 0°C, and 3.9 (± 1.3) km^2 when the temperature was below 0°C. Male fishers tended to abandon their established home ranges during the spring, and mortality was markedly higher during this season. Selection of habitat types by fishers was determined by comparing habitat characteristics at known fisher-use locations to adjacent areas that were randomly selected. Fishers used deciduous forest cover in greater proportion than its availability throughout the year and were rarely found in areas with little or no cover. Fisher were most commonly found in continuous forest stands and avoided woodlots (independent forested blocks of ≤2 km^2) during the fall and winter. When woodlots were used by fishers, they were significantly larger than the average size of available woodlots. A multivariate analysis of detailed characteristics of the overstory and understory within fisher home ranges indicated that the density of understory vegetation (≥25 stems/m^2) was a critical factor for habitat use. Canopy cover, slope, and canopy diversity were also important habitat characteristics.

Introduction

Before European contact the range of the fisher (*Martes pennanti*) encompassed forested regions throughout most of the Canadian provinces (Hagmeier 1956, Graham and Graham 1994). According to historical fur harvest records,

however, fisher populations declined and their distribution diminished early in this century (Banci 1989). Douglas and Strickland (1987) suggested that loss of habitat, particularly in the southern part of their range, through the cutting of forests for timber or conversion to other land uses, has reduced the occurrence of fishers. Overtrapping and the widespread use of poisons have also contributed to the reduction of fisher populations and resulted in regional extirpations (Douglas and Strickland 1987, Buskirk 1992). Today in Alberta, fishers are found primarily in northern coniferous forests (Skinner and Todd 1988); however, they probably inhabited the southern deciduous forests of the aspen parkland before European settlement (Hagmeier 1956).

Studies of habitat use by fishers have occurred primarily within coniferous or mixed-wood habitats in eastern North America (Banci 1989). Few studies have considered habitat use in deciduous-dominated forests (Leonard 1980, Arthur et al. 1989a). Previous studies suggest that fishers avoid open, hardwood-dominated forests (Clem 1977, Kelly 1977, Arthur et al. 1989a). Strickland et al. (1982) suggested fisher-use areas are most likely governed by the availability of food, but the presence of overhead cover may also be an important factor. Cover is required for denning, concealment, and escape from predators (Kelly 1977, Powell 1982). Areas with good overhead cover may reduce the accumulation of snow, which is thought to restrict the movements of fishers (de Vos 1952, Leonard 1980, Raine 1983, Krohn et al. 1995). Several studies suggest that optimum fisher habitat consists of a diversity of forest types with high interspersion and, therefore, greater prey abundance (Kelly 1977, Leonard 1980, Johnson 1984, Arthur et al. 1989a, Powell and Zielinski 1994).

Allen (1983) developed a hypothetical habitat suitability index (HSI) model for fishers to evaluate year-round habitat requirements within evergreen and deciduous forests, and forested wetlands throughout its range. This model consists of 4 variables: (1) percent tree canopy closure, (2) average dbh of overstory trees, (3) tree canopy diversity, and (4) percent of overstory composed of deciduous species. He concluded that dense stands in the later successional stages were required to provide suitable winter habitat for the fisher, and that the quality of winter/early spring habitat was the most restrictive component of the fisher's annual habitat requirements.

In March and June 1990, and August 1991, 20 radio-collared fishers were translocated into the aspen parkland region of central Alberta (Badry et al. 1993, Proulx et al. 1994). Those fishers released in March did not successfully establish themselves within the study area. They moved extensively, most likely because of the spring breeding season and the lack of vegetative cover at that time of year (Proulx et al. 1994). However, animals released in June and August adopted the new habitat immediately and remained in the vicinity of their release sites. Because information on the life history of fishers in deciduous forest is

lacking, especially in the western part of its range, this study of a translocated population provided a unique opportunity to examine the habitat requirements and behavior of these animals in a historically occupied habitat (Hagmeier 1956) and to challenge the characterization of the fisher as a species dependent upon mature to old, conifer-dominated forests (Allen 1983, Thomasma et al. 1991). Therefore, the objectives of this study were to (1) determine seasonal home range characteristics and habitat use of fishers in the aspen parkland region of Alberta, (2) compare the habitat requirements of fishers in the aspen parkland to the requirements assumed by Allen's (1983) habitat suitability model, and (3) develop habitat management recommendations, which would contribute to the survival of a viable fisher population in this area.

Study Area

This study was conducted in a 1225-km^2 area situated about 40 km east of Edmonton, Alberta, Canada (Fig. 1). This area is dominated by privately owned farms and acreages, and by disconnected public lands (Elk Island National Park, Blackfoot Recreation Area, Ministik Lake Bird Sanctuary), which experience heavy recreational use (Proulx and Pawlina 1992). The topographic relief is a highly variable "knob and kettle" pattern characterized by closely spaced hummocks separated by marshy depressions, ridges, and prairie mounds (Jennings 1983). Although there is an abundance of water-filled depressions, the study area is devoid of permanent streams or the valleys associated with such watercourses.

The study area was classified by Rowe (1972) as an outlier of the boreal mixed-wood forest, surrounded by aspen parkland. The nomenclature of the flora follows Moss (1983). The overstory vegetation is dominated by aspen poplar (*Populus tremuloides*), balsam poplar (*P. balsamifera*) and white spruce (*Picea glauca*) on elevated or well-drained sites. Mixtures of white birch (*Betula papyrifera*), black spruce (*P. mariana*), and tamarack (*Larix laricina*) are more prevalent on wet sites (Techman Ltd. 1979). The dominant shrub in the understory is beaked hazelnut (*Corylus cornuta*), but rose (*Rosa* spp.), saskatoon (*Amelanchier alnifolia*), choke cherry (*Prunus virginiana*), and pin cherry (*P. pensylvanicus*) are also common (Fargey 1982). Dense stands of willow (*Salix* spp.) and green alder (*Alnus crispa*) are commonly found around the profusion of lakes and ponds (Techman Ltd. 1979).

The study area supports various animal species typically preyed upon by fishers. The common small mammals include masked shrew (*Sorex cinereus*), deer mouse (*Peromyscus maniculatus*), and southern red-backed vole (*Clethrionomys gapperi*). Porcupine (*Erethizon dorsatum*) and snowshoe hare (*Lepus americanus*) are common, and in some years highly abundant. Also, several species of waterfowl commonly nest and rear broods in this region. The area also has a

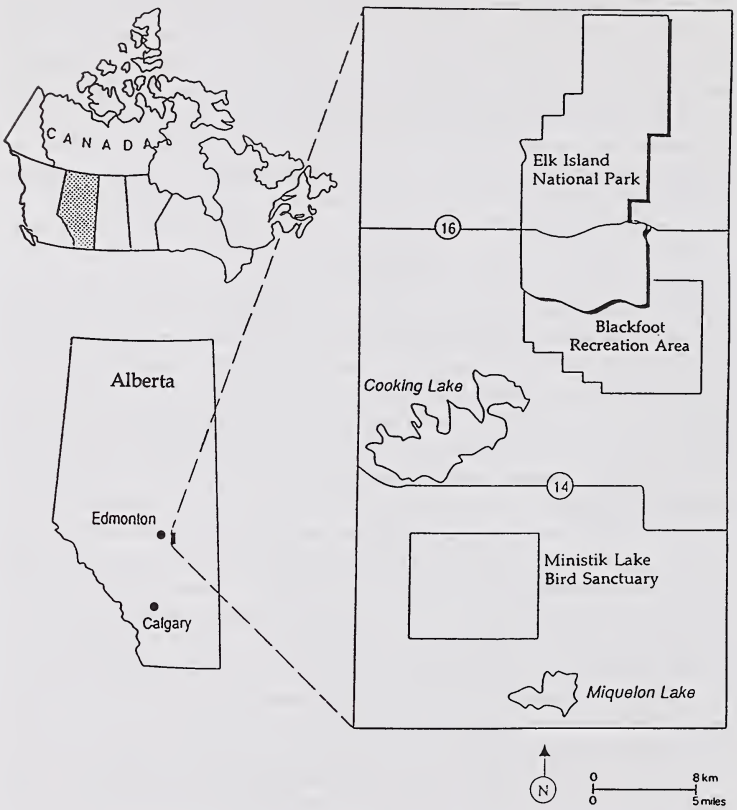

Figure 1. Fisher-release study area (modified from Proulx et al. 1994).

large population of cervids, including moose (*Alces alces*), elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*), and both wood bison (*Bison bison athabascae*) and plains bison (*B. b. bison*), which may serve as important sources of carrion for fishers.

Methods

Twenty adult (≥2 years) fishers (8 males and 12 females) were released within the study area between March 1990 and August 1992. The history of the captive fishers and methods of release were reported by Proulx et al. (1994). All fishers were ear-tagged and monitored with SMRX-3 radio transmitters with STO-1 mortality sensors (Lotek Engineering Inc., Aurora, Ontario; use of trade or manufacturing names does not imply endorsement). Locations of all fishers were recorded one or more times per week from the air or by triangulation from ground points. Triangulation involved taking 2 bearings at different locations within a 10-minute period. Telemetry error was determined to be ≤25 m from a fisher's true position when the fixes were obtained ≤1 km from the animal. At a receiver distance of 2 km, the error in correctly positioning the animal increased to 185 m (Proulx et al. 1994). Therefore, we attempted to remain ≤1 km from the animals when determining their location. Incorrect readings resulting from signal bounce (Lee et al. 1985) were discarded.

Fisher habitat use was assessed by determining the cover type at 444 independent (i.e., separated by ≥16 hours [Arthur 1987]) telemetry locations. Locations were plotted on black-and-white aerial photograph mosaics with scales that ranged from 1:10,000 to 1:40,000. These photos of the study area were taken between 1984 and 1989 and were representative of the conditions during the 1990 to 1992 sampling period. The cover type surrounding each location was classified by subjectively estimating mean canopy closure and proportion of deciduous and coniferous species present (Table 1). A minimum area of 2 ha was used to identify forest stands (Arthur et al. 1989a). Stands with an area less than 2 km^2 (200 ha) were considered woodlots, whereas larger stands were classified as continuous forest. The criterion of ≥2 km^2 to define continuous forest differs from that of Proulx et al. (1994) who used ≥1 km^2. Proulx et al. (1994) considered only initial post-release movements in their analyses. As our study progressed, however, it became evident that larger blocks, which were obviously

Table 1. Classification of forest types in the aspen parkland of Alberta.

Forest type	Characteristics
Deciduous	Total canopy ≥ 50%, deciduous species > 75%
Coniferous	Total canopy ≥ 50%, coniferous species > 75%
Mixed	Total canopy ≥ 50%, neither type > 75%
Scrub	Forest land, total canopy < 50%
Wetland	Bog, meadow, shallow marsh with emergent vegetation
Open field	No canopy, agricultural fields and pastures
Open water	Lakes, ponds and sloughs

independent of the continuous forested areas, were available and were being used by fishers. The size criterion for woodlots was therefore increased to 2 km^2. Overstory cover types were also identified for 677 randomly chosen points placed within the 1225-km^2 study area occupied by radio-collared fishers. These locations were obtained by plotting 1000 random points at a scale of 1:40,000, and overlaying them on aerial photographs of the study area. Plotted points along the perimeter often fell outside the boundaries of the study area and were discarded, leaving a total sample of 677. One male fisher travelled widely outside the study area during the spring of 1990; these locations were excluded from analysis. Stand types were classified using the same methods and criteria used in coding fisher-use locations. Habitat characteristics at fisher-use and random locations were compared using the techniques described by Marcum and Loftsgaarden (1980). Stand classifications made from aerial photos were verified by comparing photographs with areas of known cover types (Arthur et al. 1989a), and by field checking of a random subsample of 10 locations.

Annual home range areas were computed for 7 fishers (2 males and 5 females) for which we had 30 independent locations during 2 or more calendar seasons. The number of locations varied among animals (n = 32-195), but area-observation curves indicated that sample sizes were still adequate (Harris et al. 1990). For the remaining 13 animals, there were either too few locations to accurately assess their annual range use or the length of use was too short to be informative. However, when calculating home-range areas for individual seasons, those animals that were followed for only short time periods were included in the analyses.

The 95% minimum convex polygon (MCP) method (Mohr 1947, Bowen 1982) of home-range determination was used to define annual home-range areas. All home-range areas were determined using the program HOME RANGE (Ackerman et al. 1990). One-way ANOVA was used to test for effects of sex and seasons on home-range size (SAS 1985).

Detailed habitat characteristics within 2 male and 2 female fisher annual home-range areas were measured at 72 locations (36 locations per sex). Home-range areas were defined by the 95% MCP method, and fisher locations were chosen at random. At each location, percent tree canopy closure, tree canopy diversity, and percent overstory canopy composed of deciduous species (Allen 1983) were visually estimated. Overstory trees were sampled using the point-quarter distance method (Ohmann and Ream 1971). The distance from the location to each tree was measured, as was tree height and dbh. The diversity and density of understory vegetation (all live woody stems < 1 m in height) were measured by identifying the number of each plant species within a 1-m^2 plot centered on the fisher locations. The distance between downed woody debris (logs >5 mm in diameter) was also measured using the point-quarter distance method (Nordyke and Buskirk 1991) and the length and diameter of each log was recorded.

Stage of decay of each downed and dead log was characterized using the 5 decay classes described by Maser et al. (1979), with class 5 being the most advanced state of decay (Table 2). Slope and aspect were also measured at each sampling location.

Seventy random sites were selected in areas that were adjacent to fisher home-range areas, but were not known to be used by radio-collared fishers. All these locations fell within continuous forest blocks. The sites were also sampled using procedures previously discussed.

The features of occupied and random sites were compared using *t*-tests. A stepwise discriminant function analysis between the 2 types of sites was then performed to eliminate statistically redundant variables. An entry/removal criterion of $F = 0.15$ was the basis for including variables in the discriminant model. Variables identified by stepwise regression were then entered into a canonical discriminant function analysis (SAS 1985) to determine the habitat dimensions (if any) along which occupied and random sites differed, and to test the predictability of group membership (occupied or random) for each site. Variables that were excluded by stepwise regression but showed a significant *t*-value ($t \leq 0.001$) were then re-entered into the discriminant function analysis to determine if they improved the model's ability to discriminate between sites. Because occupied and random sites were not sampled at the same frequency (72 fisher and 70 random), the classification procedure was based on prior probabilities equal to

Table 2. Five stages of structural change of logs with age, as described by Maser et al. (1979).

Stage	Description
1	Essentially sound with support points intact.
2	Weakened and sagging slightly but still elevated on support points; duff and soil building up on the sides.
3	Bark loosened, support points are gone and the log sags.
4	Log completely on the ground and may be partially buried, with the inside soft enough for small mammals to burrow.
5	Logs soft and powdery, partially buried and with long-established burrow systems, both within and underneath, used primarily by small mammals.

the sample sizes of each site type. All statistical procedures were performed using PC-SAS software (SAS 1985). Probability values ≤ 0.05 were considered statistically significant.

Results

Sixteen fishers (6 males and 10 females) were located 1006 times between March 14, 1990 and September 15, 1992. No locations were obtained for 1 male that escaped during the acclimation period and was found dead 1 week later, or for 1 male and 2 females that slipped their radio-collars shortly after being released.

Home-Range Areas

Using the MCP method of home-range determination, the mean annual home range of 5 females was 14.9 ± 3.5 (SE) km² and did not differ statistically from that of the 2 males (24.3 ± 11.1 km²) ($F = 1.29$, df = 6, $P = 0.31$; Table 3, Fig. 2).

The cold (<0°C) season extended from 14 to 25 March 1990 and from 1 November 1990 to 27 March 1991. The warm season (>0°C) extended from 26 March to 31 October 1990 and from 28 March to 15 October 1991. Sample sizes based on temperature-related measurements ranged from 11-50 locations ($n = 4$

Table 3. The mean home-range sizes of adult fishers in central Alberta.

Variable		*n*	Mean home range (km², ± SE)
Sex*			
	Male	2	24.3 ± 11.1
	Female	5	14.9 ± 3.5
Temperature**			
	Warm (≥0°C)	9 (2M + 7F)	14.5 ± 3.1
	Cold (<0°C)	4 (1M + 3F)	3.9 ± 1.3
Snow Pack**			
	No snow	10 (2M + 8F)	12.9 ± 3.1
	Snow	5 (1M + 4F)	6.1 ± 1.1

M = male; F = female.

* All seasons combined.

** Sexes combined.

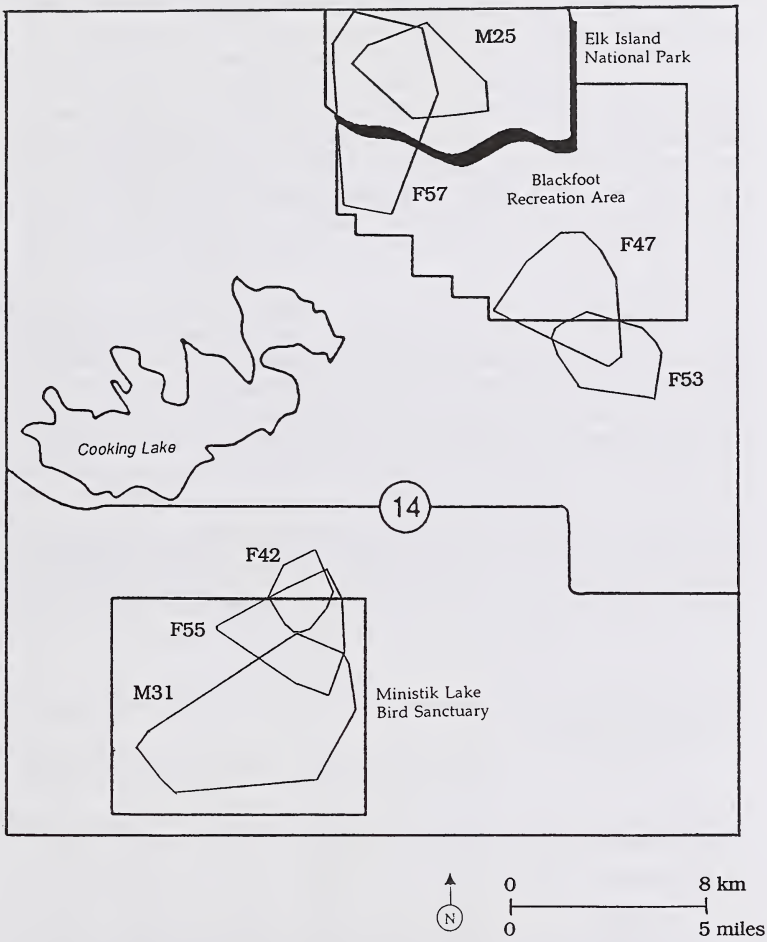

Figure 2. The distribution and size of annual home range areas (95% MCP) for 2 male (M25 and M31) and 5 female (F42, F47, F53, F55, and F57) fishers in central Alberta.

fishers) for the cold season and 31-107 locations (n = 9) for the warm season. When the temperature was below freezing, home ranges averaged 3.9 ± 1.3 km². Above 0°C, home ranges were significantly larger (F = 4.67, df = 3, P = 0.05) and averaged 14.5 ± 3.1 km² (Table 3).

A continuous snowpack was present on the study area from 14 March to 30 April 1990, and from 1 November to 31 March 1991. The area was snow-free from 1 May to 31 October 1990 and from 1 April to 16 October 1991. In the presence of snow, the mean home range of 5 fishers (31 to 51 locations/fisher) was 6.1 ± 1.1 km². In the absence of snow, the home range of 10 fishers (11 to 107 locations/fisher) was 12.9 ± 3.1 km². The difference between these means is not significant (F = 2.19, df = 14, P = 0.16; Table 3).

Macro-Habitat Use

Fisher locations (n = 444) did not occur in proportion to cover-type availability (n = 677; χ^2 = 368.6, df = 6, $P < 0.001$). Fishers used deciduous stands more than their relative availability, whereas coniferous, mixed, and wetland cover types were used in proportion to their availability. Scrub, open field and open water were used less than expected based on their availability. Because it has been previously documented that fishers avoid open areas (de Vos 1952, Ingram 1973, Kelly 1977, Powell 1982, Arthur et al. 1989a), and data from this study reaffirmed this conclusion, the categories of open field and open water were removed (n = 10 fisher locations and 310 random points) and the data were reanalyzed to compare habitat use among the 5 remaining forest types (Table 4). Re-analysis indicated that fisher use did not occur in proportion to the availability of forest types (χ^2 = 119.98, df = 4, $P < 0.001$). Deciduous stands were used more than expected ($P < 0.05$), and mixed and wetland habitats were used in

Table 4. Cover types at random and fisher locations (open-field and open-water categories deleted).

Location	n	Deciduous %	Coniferous %	Mixed %	Scrub %	Wetland %
Random locations	367	40.9	5.5	9.0	27.5	17.2
Fisher locations	434	74.2[a]	1.2[c]	7.1[b]	4.8[c]	12.7[b]
Males	87	72.4[a]	4.6[b]	8.1[b]	2.3[c]	12.6[b]
Females	347	74.6[a]	0.3[c]	6.9[b]	5.5[c]	12.7[b]

[a] Preferred.
[b] Used in proportion to availability.
[c] Avoided.

proportion to their availability. Coniferous stands and scrub were used less than expected. Both males (87 locations) and females (347 locations) used deciduous stands more than expected and used scrub less than expected. However, females used coniferous stands less than expected, whereas male fishers used them in proportion to their availability.

Both male and female fishers used continuous forest blocks more than expected based on their availability ($P < 0.01$; Table 5). Animals were located in continuous forest 71.9% of the time, whereas only 17.1% of random locations fell within continuous forest stands. When fishers utilized woodlots, they tended to use stands that were larger than the average available ($P < 0.01$). Fishers were located in woodlots 46 times (10.3%) and the mean stand size was 0.40 ± 0.08 km^2. Eighty-five random locations (12.6%) occurred in woodlots with a mean stand size of 0.18 ± 0.03 km^2.

Micro-Habitat Use

Based on univariate tests, fisher locations had higher values of canopy cover ($P < 0.001$), total woody stems in the understory ($P < 0.001$), slope ($P = 0.002$), diameter of downed woody debris ($P = 0.01$), percent deciduous species in the overstory ($P = 0.026$), tree height ($P = 0.027$), and dbh ($P = 0.046$) than did random locations (Table 6).

Table 5. Percentage of random and fisher locations occurring in continuous forest stands and woodlots (all seasons combined).

	Continuous Forest (≥2 km^2)		Woodlot (<2 km^2)		
Location	*n*	%	*n*	%	mean size (km^2 ± SE)
Random locations	116	17.1	85	12.6	0.18 ± 0.03
Fisher locations	312	71.9[a]	46	10.3[b]	0.40 ± 0.08[a]
Males	74	85.1[a]	8	9.2[b]	0.32 ± 0.10[a]
Females	238	68.6[a]	38	11.0[b]	0.48 ± 0.10[a]

[a] Preferred habitat or woodlot size significantly larger than random ($P < 0.01$).
[b] Used in proportion to availability, or woodlot size not significantly different from random ($P < 0.05$).

Table 6. Habitat features of fisher and random locations.

Habitat variable	Mean (± SE) Fisher location	Random location	*P*
Overstory			
Canopy cover[a]	1.7 ± 0.05	1.3 ± 0.06	< 0.001
Canopy diversity[b]	2.2 ± 0.08	2.1 ± 0.06	0.138
Deciduous species (%)	96.2 ± 1.31	99.3 ± 0.40	0.026
Tree height (m)	6.3 ± 0.71	4.4 ± 0.47	0.027
dbh (mm)	65.5 ± 8.69	44.0 ± 6.05	0.046
Distance between trees (cm)	491.0 ± 133.64	214.7 ± 71.16	0.072
Understory			
Woody stem density (/m^2)	25.3 ± 1.37	12.5 ± 1.05	< 0.001
Debris length (cm)	178.0 ± 30.12	135.2 ± 14.66	0.207
Debris diameter (mm)	28.1 ± 2.89	19.2 ± 1.75	0.010
Distance between debris (cm)	138.6 ± 47.18	113.8 ± 48.07	0.714
Stage of decay (Table 2)	3.1 ± 0.09	2.9 ± 0.08	0.125
Topography			
Slope (°)	5.8 ± 0.68	1.9 ± 0.31	0.002
Aspect (N = 0°)	94.5 ± 4.42	90.0 ± 4.77	0.476

[a] 1 = 0-50% closure, 2 = >50% closure.
[b] 1 = single-storied stand, 2 = two-storied stand, 3 = multi-storied stand.

A stepwise discriminant function analysis of the 13 habitat variables identified 5 potential discriminators (canopy cover, canopy diversity, slope, distance between trees, and stage of decay of downed woody debris) of occupied and random sites (Table 7). A test for homogeneity of within-group covariance matrices (Morrison 1976) was rejected (χ^2 = 74.7, df = 15, $P < 0.001$). Therefore, the canonical analysis was performed using a quadratic discriminant function (i.e., using the within-group, rather than pooled, covariance matrix) (SAS 1985). The discriminant function based on these 5 habitat variables was significant (F = 13.2, 5; df = 132; $P < 0.001$), and the relationship between discriminant scores calculated from the quadratic function and group membership was moderate (r = 0.67). The overall classification success rate of the quadratic discriminant function was <70%.

Table 7. Potential discriminators between fisher and random locations, as determined by stepwise discriminant function analysis.

Habitat variable	Step entered	Partial R^2	F	P
Canopy cover	1	0.11	16.45	< 0.001
Distance between trees	2	0.07	9.68	0.002
Canopy diversity	3	0.09	12.90	< 0.001
Slope	4	0.08	12.31	< 0.001
Stage of decay	5	0.07	10.60	0.001

Habitat variables identified as significant by univariate analysis were used in a second discriminant function analysis in an attempt to improve the ability to discriminate between fisher and random locations. The discriminant function based on 4 habitat variables (woody stem density, canopy cover, canopy diversity, and slope) was significant ($F = 15.8, 4$; df = 137; $P < 0.001$), and the relation between discriminant scores and group membership was also moderate ($r = 0.68$). Occupied and random sites were best discriminated by the density of woody stems in the understory (Table 8). Fisher-use areas contained a greater density of total stems (25.3 ± 1.0/m²) than did random locations (12.5 ± 1.4/m²). In addition, canopy cover, slope, and canopy diversity were all greater at occupied sites than at random sites (Table 6). The quadratic discriminant function had an overall classification success rate of 81.0%. Based on the 4 habitat variables considered, 57 of 72 (79.2%) occupied sites, and 58 of 70 (82.9%) random sites were correctly classified. Because the data used to generate the discriminant model were also used in the classification procedure, these classification rates may be slightly inflated (Klecka 1980).

Table 8. Pooled within-groups correlations between canonical discriminant function scores and discriminating variables of fisher and random locations.

Habitat variable	Correlation coefficient
Woody stem density	0.70
Canopy cover	0.62
Slope	0.39
Canopy diversity	0.19

Discussion

As suggested by Allen's (1983) habitat suitability index model, forest stands with a well-developed and diversified canopy, and high dbh, were used by fishers in the aspen parkland of Alberta. However, contrary to Allen's (1983) model, fishers translocated into our study sites in the aspen parkland used deciduous stands more than expected. In addition, although previous studies (e.g., deVos 1952, Clem 1977, Raine 1981, Johnson 1984) used overstory type and density to identify fisher habitats, this study indicates that the density of woody stems in the understory is also an important parameter that should not be overlooked.

Our results suggest that fisher habitat modelling should take the regional needs of the species into consideration. The presence of dense coniferous cover during winter may not be necessary in the aspen parkland region if temperatures and snowfall are relatively mild. A dense understory may compensate for a lack of conifers by providing fishers with homeothermic advantages (Buskirk et al. 1989) and access to prey (Powell and Zielinski 1994). Our findings seem to support the work of Strickland et al. (1982) and Arthur et al. (1989a) who concluded that optimum fisher habitat may consist of any forested area that provides a suitable prey base. Our results also suggest that parameters such as forest type and canopy cover are not sufficiently reliable indicators of suitable habitat for fishers. Field sampling of the understory in aspen forest stands and the evaluation of site-specific structural characteristics appear to be important for properly assessing the potential of an area for fishers.

Our estimates of annual home-range size of fishers varied greatly but were within the reported ranges of 14.0-30.9 km^2 for adult males and 3.6-16.3 km^2 for adult females (Kelly 1977, Buck et al. 1979, Johnson 1984, Arthur et al. 1989b). Fishers travel greater distances when the weather is above 0°C. Kelly (1977) also found that both sexes inhabited relatively small home ranges in the month of January, and concluded that severe weather conditions caused them to spend more time in their den. He speculated that this was a strategy for reducing thermal stress. Although fishers may not need extensive coniferous cover to survive the winter in the aspen parkland, snow did impact on their movements as previously suggested by Raine (1983). By remaining inactive at times when movements are restricted, and prey may be less available or perhaps more difficult to catch, fishers are able to conserve energy.

It is difficult to interpret the relatively low use of coniferous stands by females because the occurrence of this habitat type was low in our study area. Most of the coniferous cover was found in the northern end of the study area (in Elk Island National Park), which our radio-collared fishers never inhabited. This lack of use may be due to the high density of large ungulates (moose, elk and bison) in this park. It is readily apparent that browsing and trampling of the surface

vegetation by the high numbers of ungulates has resulted in a sparse understory with a poor prey population (Proulx et al., unpublished data). In general, the lack of use may be due to the shortage of prey. The other coniferous-dominated sites in the study area are wet or bog sites covered by black spruce. Coulter (1966) found that low-lying coniferous forests containing a high proportion of bogs did not support high populations of fishers. The greater use of coniferous forest by males than females, when compared to the proportion of habitat available, may have been due to the males' greater mobility (Proulx et al. 1994). By covering a large area, males have a greater chance of encountering the relatively rare patches of coniferous cover, as compared to the more sedentary females.

Few studies of habitat selection by fishers have considered stand insularity as a habitat variable (Rosenberg and Raphael 1986, Buskirk 1992). The size and spacing of woodlots in fragmented habitats may have an important impact on animals in search of mates, new food resources, or unoccupied yet suitable habitat. Rosenberg and Raphael (1986) inventoried terrestrial vertebrates in Douglas-fir (*Pseudotsuga menziesii*) forests in northwestern California and found that fishers were relatively sensitive to forest fragmentation. The presence of fishers was most highly correlated with stand insularity. A weak, but positive, association between stand area and fisher occurrence was also noted in this study, with fisher use decreasing sharply in frequency of occurrence in stands < 100 ha. In central Alberta, fishers preferred continuous forest but their frequency of occurrence in insular stands, or woodlots, was in proportion to the availability. They did, however, selectively use woodlots with a larger mean area than that of available woodlots. Larger stands presumably offer greater cover and a higher abundance of prey species. The relatively large amount of edge, or ecotonal habitat, found around large woodlots may also be important to the foraging success of fishers (Kelly 1977).

Management Implications

Because fishers have probably been absent from the aspen parkland of Alberta for almost a century, nothing is known about their life history and behavior in this habitat type. Large expanses of coniferous cover appear to be unnecessary. However, continuous tracts of unfragmented deciduous forest with a high tree canopy and a well-developed understory must be retained to give fishers access to areas large enough to establish their home ranges and to a prey base large enough to satisfy their needs. In addition, this habitat must be sufficiently covered with trees to provide protection from both ground and aerial predation. Last, it must be big enough to support a population of females.

For the fisher population in central Alberta to expand, it will be necessary to develop and retain large woodlots and treed travel corridors for dispersal and

exploratory movements. Arthur et al. (1993) observed that the dispersal distance of fishers in Maine was quite small ($\bar{x}$ = 10.8 km for males and 11.2 km for females) suggesting that they would not readily recolonize large areas from which they had been extirpated. The fisher translocation area in this study is well removed from northern fisher populations inhabiting the boreal forest and fisher immigration is very unlikely. Short dispersal distances also suggest that maintaining viable fisher populations may be difficult in areas where suitable habitat patches are small and widely spaced. By maintaining large expanses of habitat, connected by a mosaic of forested patches within agricultural areas, fishers will be provided with suitable and safe travel routes, which may reduce mortality associated with the crossing of open areas during long-distance movements (see Proulx et al. 1994).

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LANDSCAPE-LEVEL SELECTIVITY BY FISHERS IN SOUTH-CENTRAL BRITISH COLUMBIA

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Abstract: We examined landscape-level selectivity by fishers (*Martes pennanti*) in south-central British Columbia from December 1990 to May 1993. Fifteen fishers were live-trapped, radio-collared, and translocated into the study area. Landscape-level selectivity was determined by comparing the availability of stands within the landscape to the following: (1) those used by 15 transient fishers (13 F, 2 M) prior to home-range establishment, and (2) the habitat composition of the seasonal home ranges of 9 resident fishers (7 F, 2 M). While they were transient, the translocated fishers used non-vegetated and early seral stage stands (<10 years) significantly less frequently than expected based on availability within the landscape. They used the young forests (41-80 years) and coniferous forests significantly more frequently than expected. Translocated fishers moved extensively before establishing home ranges. Large rivers and topography were not barriers to movement. Selectivity for the inclusion of some forest phases within home ranges was exhibited by some individuals, but there were no consistent trends. Our research has implications for the maintenance of fisher populations in south-central British Columbia because increases in the proportion of early seral stages in the region caused by habitat alteration, such as forest harvesting, may reduce the suitability of the landscape as dispersal habitat for fishers.

Introduction

Like most other *Martes* species, fishers (*M. pennanti*) occur primarily in forested landscapes and often prefer late-successional forests over younger seral stages (e.g., Clem 1977, Jones and Garton 1994). Although in eastern portions of their range in North America fishers may not require late-successional stands (Arthur et al. 1989, Krohn et al. 1995), fishers in western coniferous forests may rely on the structures and ecological processes associated with late successional stands to fulfill many of their life requirements (Ruggiero et al. 1994).

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A landscape, by our definition, is a large unit of land that contains a series of watersheds and includes a variety of different vegetation types. In forested landscapes, these vegetation types are generally referred to as stands. Selection of habitat within the landscape can occur during 2 periods in the life of fishers: when fishers are transient, and when they are resident. While transient, fishers make landscape-level decisions when selecting stands to use within the landscape. Habitat selection at the landscape level can also be examined by comparing the stand composition of home ranges occupied by resident fishers with the stand composition of the landscape. The stand composition of the home ranges of resident fishers is the result of landscape-level selectivity made by fishers when they established or inherited their home ranges. During both transient and resident periods, habitat selection occurs at the landscape scale and is constrained by the composition of the landscape.

Several population processes occur at the landscape spatial scale and are important for the persistence of fisher populations. For an area to support a viable population of a species, individuals must successfully navigate the landscape and establish home ranges, and survive and reproduce in these new ranges (Ebenhard 1991). Through habitat alteration, modifications to the structure and composition of the forested landscape may have detrimental effects on the rates of population processes within and among fisher populations. Examination of landscape-level selection provides insight into the viability of fisher populations within a particular area.

To conserve fishers in the increasingly altered and fragmented landscapes of central British Columbia, several aspects of the habitat requirements of fishers at the landscape scale need to be described. Once these requirements have been identified, ecosystem managers may be able to modify habitat alterations so that they are more compatible with the needs of fishers.

We examined habitat selection in the landscape of the dry-warm subzone of the Sub-Boreal Spruce biogeoclimatic zone of south-central British Columbia by comparing the availability of stands in the landscape to the use of stands by transient fishers before home-range establishment and to the stand composition of fisher home ranges for both translocated and resident fishers. If landscape-level selection occurs, fishers should show selectivity in their use of stands while they are transient. Furthermore, if landscape-level selection occurs, stands that are included within the home ranges of fishers should be different from their availability in the landscape.

Study Area

The study area covered 1500 km^2 and was centred 65 km northeast of Williams Lake, British Columbia. The boundary of the study area was defined by

the extent of the dry-warm subzone of the Sub-Boreal Spruce (SBSdw) biogeoclimatic zone. The Sub-Boreal Spruce zone is heavily forested and dominates the central interior of British Columbia. It generally occurs from valley bottoms up to 1300 m in elevation (Meidinger et al. 1991). The climate of the Sub-Boreal Spruce zone is continental and is characterized by severe, snowy winters and relatively warm, moist, and short summers. Mean annual temperatures in the study area range from 3.4° to 3.7°C (B.C. Ministry of Forests 1987).

The study area consisted of gently rolling hills, with elevations ranging between 750 and 1250 m. Upper elevations on the western border of the study area were transitional to the moist-cool subzone of the Sub-Boreal Spruce zone, which occurs on hills above 1300 m (B.C. Ministry of Forests 1987). The study area was bounded on the south and southwest by the drier Sub-Boreal Pine-Spruce and Interior Douglas-fir zones, and on the east by the Interior Cedar-Hemlock zone.

Forests were dominated by Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and hybrid white spruce (*Picea engelmannii* x *glauca*), with trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and black cottonwood (*Populus balsamifera trichocarpa*) occurring as minor components. The SBSdw has a natural disturbance regime of frequent, large-scale burns on a cycle of about 300 years, with most stands burning every 100 years (R. Coupé, B.C. Ministry of Forests, pers. commun.). Harvesting of late successional forests, using a variety of techniques, has occurred over the past 40 years. The result is a mosaic of seral stages and stand types throughout the study area. Land clearing for cattle grazing and cultivation has occurred along most valley bottoms.

Fishers have been present historically throughout the study area and have been trapped since at least 1860 (S. Nicol, registered trapline owner, pers. commun.). The trapping season in this area is open from the beginning of November through to mid-February, but most of the trappers in the study area agreed to suspend trapping of martens and fishers, or use live traps in areas with resident fishers, during the course of the study. A small (likely fewer than 7 fishers), low-density population of fishers inhabited the study area before our study began.

Methods

Trappers live-trapped fishers during the early winters of 1990-91 and 1991-92. All of the fishers were caught in 30 × 30 × 100-cm box livetrap sets in the Chilcotin River drainage, approximately 300 km west of the study area. The trappers transported each fisher in a covered boxtrap from their capture sites to the B.C. Ministry of Environment facilities at Williams Lake. Upon arrival, we monitored the fishers for several hours to assess their physical condition.

We anaesthetized each fisher for 45-90 min using a 10:1 ketamine hydrochloride:xylazine hydrochloride mixture administered at 22 mg/kg body weight, injected intramuscularly. When required, we injected the fishers with an additional 15 mg/kg of ketamine to maintain anaesthesia. We weighed, sexed, and measured each fisher. We removed a first premolar from healthy fishers for cementum annuli analysis (Strickland et al. 1982), whereas we classed fishers that had worn teeth or lingual erosions as adult or juvenile by palpitating the sagittal crest (Powell 1982). Fishers that were less than 1 year of age were considered juveniles, whereas those >1 year were considered adults. We fitted fishers with mortality-sensing, whip antennae radio-collars. We "soft-released" (Davis 1983, Proulx et al. 1994) 14 fishers and "hard-released" 1 fisher at different locations in the study area. In addition to the translocated animals, we live-trapped resident fishers within the study area and fitted them with radio-collars.

Immediately following release, we relocated each fisher twice per week from the air, and when possible, located them daily from the ground. We relocated fishers using standard ground and aerial telemetry procedures (White and Garrot 1990). We estimated ground locations using Locate II software (Nams 1991), which uses the maximum likelihood estimator to calculate transmitter locations and error polygons. We calculated the minimum total distance that each transient fisher could have travelled while transient by tallying the straight-line distances between successive locations during this period. The area traversed by each translocated fisher was calculated as the area of the 100% convex polygon (Mohr 1947) created by all locations obtained during the transient phase. We considered home ranges to be established when translocated fishers began to exhibit permanent site fidelity (Weir 1995).

We estimated home ranges using the adaptive kernel technique, with h selected by cross validation and the smoothing parameter chosen by the least squares method (Worton 1989, Seaman and Powell 1991). We determined the boundary of each home range from the 90% isopleth of the utilization distribution (UD). We estimated home ranges from a minimum of 20 independent locations.

We delineated stand types within the study area using the biophysical classification system presented by Lea (1992). We classified stands according to biophysical unit, seral stage, and forest phase. Stands were assigned 1 of 7 seral stages ranging from non-vegetated to old growth, and 1 of 4 forest phases (coniferous, deciduous, mixed coniferous-deciduous, or non-forested). We delineated biophysical units using ecosystem associations as determined by Clements (1991) and B.C. Ministry of Forests (1987). We considered stands as relatively homogeneous assemblages of habitat with respect to coarse woody debris, closure of vegetation strata, and other structural attributes.

We estimated the availability of each stand type in the landscape of the SBSdw from 1015 random locations in the study area, using Marcum and Loftsgaarden's

(1980) non-mapping technique. Because of financial constraints, we were unable to map the entire study area. Consequently, biophysical mapping was performed for 405 km^2 of the study area, covering the areas in which the home ranges of 9 of 12 fishers occurred. We estimated stand types for aerial locations and for ground telemetry locations at which 95% error polygons (Nams and Boutin 1991) were less than 1.5 ha.

Landscape-level habitat selectivity was assessed during 2 periods: the transient phase and the resident phase (i.e., after home-range establishment). Selectivity during the transient phase was determined by comparing the use of stands prior to home-range establishment to the availability of these stands in the landscape. We compared the use of stands by transient fishers to the availability of those stands, which were classified by seral stage, forest phase, and site association. For the resident period, we overlaid seasonal home ranges on biophysical maps of the study area and used a digital planimeter to estimate the percentage of each stand type within each home range. We considered fishers that were translocated and subsequently established home ranges and non-translocated fishers as residents for this analysis. We assumed that the processes for selecting home ranges were similar among translocated and non-translocated fishers.

We performed chi-square goodness-of-fit tests and Bonferroni-adjusted *Z*-tests (Neu et al. 1974) on locations pooled for all fishers while transient. We determined trends in landscape selectivity among fishers by comparing the mean Vanderploeg and Scavia's relativized electivity index (Lechowicz 1982) for each stand type in the home range of each fisher to 0 (no selectivity) using *t*-tests. We also compared the composition of each home range to availabilities using chi-square goodness of fit and Bonferroni-adjusted *Z*-tests (Neu et al. 1974). We limited analyses to those stand types that constituted at least 5% of the landscape to eliminate interpretation problems associated with high use-availability ratios resulting from spurious inclusion of rare stand types within the landscape. We set the acceptable type I error at 0.05.

Results

We translocated 15 fishers over 2 winters. We released 5 females (2 juvenile, 3 adult) in the winter of 1990-91, and 10 fishers (3 juvenile F, 5 adult F, 1 juvenile M, 1 adult M) in early 1992 (Table 1). In addition, we live-trapped and radio-collared 7 resident fishers within the study area. Two resident females were juveniles at first capture; the others were adults (4 F, 1 M). We located fishers that had functioning radio-collars from 15 December 1990 to 30 May 1993.

The translocated fishers wandered extensively prior to establishing home ranges. While transient, several fishers wandered through areas of more than 700

Table 1. Movements prior to home-range establishment of fishers translocated into the SBSdw subzone, 1990-1992.

ID	Release date	*n*	Duration of transiency (days)	Minimum total distance moved (km)	Area traversed (km^2)
F290	11 Feb 1992	16	54	132.4	301.7
F350	02 Mar 1992	8	37	136.0	743.7
F390	15 Feb 1992	14	57	172.3	733.8
F598	13 Dec 1990	22	90	87.2	169.2
F700	23 Jan 1991	5	9	12.5	50.2
F805	25 Nov 1990	34	197	276.3	990.3
F917	10 Jan 1991	17	67	93.8	108.6
M380	27 Jan 1992	11	69	1055.5	188.9
M450	02 Mar 1992	6	34	1038.1	987.0

ID: F = female; M = male.
n: Number of radiolocations obtained while fisher was transient.

km^2 and most of the fishers travelled at least 100 km in total distance before establishing a home range (Table 1). Before establishing home ranges, female fishers traversed an average area of 442.5 km^2 (SE = 141, n =7), whereas males traversed an average of 1438.0 km^2 (SE = 451, n = 2). The fishers were able to move long distances between locations; 1 male fisher moved 53.2 km in less than 68 h. During the transient phase, fishers crossed the Quesnel River (minimum flow = 99 m^3/s in January) on several occasions, and many of its smaller tributaries as well. The mean established home ranges (± SE) of female fishers (90% UD) were 26.4 ± 9.2 km^2 (annual, n = 5), 33.0 ± 10.7 km^2 (summer, n = 8), 32.3 ± 18.3 km^2 (autumn, n = 3) and 25.0 ± 2.6 km^2 (winter, n = 6).

We determined landscape use from 116 locations of 15 translocated fishers during their transient phase. We located transient fishers from their respective release dates until either failure of the radio transmitter of each fisher or establishment of their home ranges. All but 1 of the translocated fishers that we monitored for longer than 2 months established home ranges by the April following release (Weir 1995). When we classified stands by seral stage, transient fishers used non-vegetated and early seral stage stands (<10 years) less frequently than expected based upon availability within the landscape, but used the young forest stage (41-80 years) more frequently than expected ($\chi^2 = 23.87$, df = 4, $P < 0.001$)

Table 2. Selectivity of stands by translocated fishers while transient in the SBSdw subzone during winter 1990-1992, as classified by seral stage. Transient fishers avoided early seral stages and selected later successional forests more frequently than expected (n = 116 locations).

Seral stage	Stand age (years)	Proportion available (p_a)	Proportion used (p_u)	Bonferroni-adjusted significance interval[a]
Non-vegetated	0	0.03	0.00	0[b]
Herb-Shrub	1-10	0.23	0.06	0.002 p_u 0.119[b]
Pole-Sapling	11-40	0.09	0.10	0.027 p_u 0.170
Young Forest	41-80	0.33	0.49	0.359 p_u 0.598[b]
Mature Forest	81-250	0.29	0.36	0.250 p_u 0.480

[a] Interval over which the proportion used is not significantly different from the proportion available at $\propto$ = 0.05.
[b] Significant difference between p_a and p_u.

(Table 2). When we classified stands by forest phase, transient fishers used non-forested stands less frequently than expected, but used coniferous forests more frequently than expected ($\chi^2 = 41.35$, df = 3, $P < 0.001$) (Table 3).

We also determined landscape selectivity by examining the stand composition of seasonal home ranges of resident fishers. Only 9 of 12 resident fishers (7 F, 2 M) were included in this analysis because some of the translocated fishers established home ranges outside of the mapped areas. We did not detect any significant departures from random inclusion of stands within seasonal home ranges of fishers for stands classified by biophysical unit, seral stage or forest phase.

Although trends in selectivity were not consistent, the proportion of stands in the seasonal home ranges of several fishers differed significantly from availability. The composition of 4 of the 16 seasonal home ranges were significantly different from expected, based upon availability, when stands were classified by forest phase. However, the inclusion of the different forest phases in seasonal home ranges varied among fishers (Table 4).

Our study area was a fine-grained mosaic of stands. As a measure of granularity, we developed an index based on the mean stand area compared to home-range area. The mean granularity ratio (mean stand area:home-range area) for the fishers that we examined was 0.011 (SE = 0.040, n = 7) during summer, 0.010 (SE = 0.039, n = 3) during autumn, and 0.009 (SE = 0.002, n = 7) during winter. On average, there were 149 stands within the home ranges of fishers during summer (SE = 44, n = 3), 170 during autumn (SE = 93, n = 3), and 147 stands during winter (SE = 37, n = 7).

Table 3. Selectivity of stands by translocated fishers while transient in the SBSdw subzone during winter 1990-1992, as classified by forest phase. Transient fishers avoided early seral stages and selected later successional forests more frequently than expected (n = 116 locations).

Forest phase	Proportion available (p_a)	Proportion used (p_u)	Bonferroni-adjusted significance interval[a]
Non-forested	0.27	0.06	0.002 p_u 0.115[b]
Deciduous	0.03	0.04	0.000 p_u 0.080
Mixed coniferous/deciduous	0.38	0.33	0.220 p_u 0.445
Coniferous	0.32	0.56	0.446 p_u 0.683[b]

[a] Interval over which the proportion used is not significantly different from the proportion available at $\propto = 0.05$.
[b] Significant difference between p_a and p_u.

Discussion

During transiency, translocated fishers were able to access the entire landscape of the SBSdw within the study area. Most translocated fishers wandered extensively following release, but all established home ranges within the SBSdw. Initial movements away from their release sites were large-scale (>6 km), and large rivers and elevation changes of 700 m were not barriers to movement.

While transient, fishers avoided non-forested and early seral stages, which have little overhead canopy closure. This selectivity is consistent with the findings of other studies (Kelly 1977, Powell 1977, Arthur 1987), which suggest that fishers require overhead cover. The preference for overhead cover may also

Table 4. Landscape-level selectivity of forest phase (SBSdw subzone, 1990-1993) in seasonal home ranges of fishers that exhibited selectivity. A consistent trend in the composition of seasonal home ranges was not evident.

ID	Season	Selection for	Avoidance of
F290	Summer	Coniferous	Deciduous, Mixed
F350	Summer	Mixed	Coniferous
F770	Winter	Deciduous, Non-forested	Coniferous, Mixed
F855	Autumn	Coniferous, Non-forested	Mixed

F = female

explain the avoidance of mixed forest stands while the fishers were transient. Proulx et al. (1994) hypothesized that deciduous vegetation cover affected the movement patterns of translocated fishers in central Alberta. In our study, the fishers were released during midwinter, when deciduous trees were bare of leaves. The mixed forest stands had little overhead cover during winter, which may have contributed to their avoidance by fishers. The affinity exhibited by fishers for stands with overhead cover was revealed by the selection of the young forest seral stage and coniferous forests. However, other factors, such as differential mobility because of snow quality or prey vulnerability may have contributed to the patterns of habitat use that we observed.

Ideally, stand types included within a home range should maximize the fitness of the individual (Buskirk and Powell 1994). Maximizing the proportion of good stands comprising the home range, and minimizing the inclusion of poor and marginal stands, should result in increased survival and reproduction of the individual, because energy costs of acquiring resources are lower in good habitat than in poor or marginal habitats (Thompson and Harestad 1994).

The lack of selectivity for inclusion of specific stand types within the home ranges of resident fishers in our study may be a consequence, in part, of the nature of the landscape in the SBSdw. The granularity of the landscape, the ratio of the average habitat unit (i.e., stand) size to home-range size, may affect the ability of researchers to detect selectivity at the landscape scale. In fine-grained landscapes, where stands are small relative to home-range size, landscape-level selectivity is unlikely to be detected because individual animals are not constrained by access to suitable habitat. Because the landscape is composed of many small interspersed stands, any point in the landscape is not far from suitable habitat. In coarse-grained landscapes, however, landscape-level selectivity is likely to occur because animals must search for and include within their home range areas of suitable habitat to ensure access to these stands.

In the SBSdw, fishers may not have exhibited consistent trends in landscape-level selection because habitat granularity was too fine when we examined habitat selectivity using the biophysical habitat classification system. If habitat granularity was coarser and stands were larger, mean stand size relative to home-range size would be greater and selectivity may have become apparent. For example, fishers avoid areas with no overhead cover (Kelly 1977, Powell 1977). Therefore, with respect to overhead cover, had stands in our study area been large homogenous areas, the mean stand size would be large relative to home-range size, and fishers would be expected to include open areas less frequently than expected within their home ranges. However, our study area was a fine-grained mosaic of stands. As the mean size of stands decreases (i.e., granularity of the landscape decreases), fishers likely have to include unsuitable stands within their home ranges to ensure access to stands of suitable habitat.

One other possible explanation for the lack of selectivity for the inclusion of stand types within the home ranges of fishers may be that fishers select for a diversity of habitats. This alternative hypothesis is also consistent with our observations. Diversity of habitats within a home range could be met in many places in our study area. Because of the habitat granularity characteristics of our study area, we cannot discriminate between these 2 hypotheses.

Management Implications

Fragmentation and alteration of continuous forest landscapes has several potential effects on wildlife populations. Although generalist species are better able to cope with alterations of the landscape (Ebenhard 1991), some habitat specialists, as fishers appear to be in south-central British Columbia (Weir 1995), are dependent upon structural elements associated with late successional forests to fulfill their life requisites. Fracturing of the landscape can affect the dispersal capability of these specialist species (Harris 1984) and decrease populations to points where stochastic events can cause local extinctions (Gilpin and Soule 1986, Hanski and Gilpin 1991). Conservation of the processes of dispersal and home-range establishment are necessary for the persistence of wildlife within a fragmented and altered landscape.

Dispersal habitat is required for the movement of animals through the landscape, which is important for maintaining dispersion of genes through the environment. The rate at which transients are able to successfully navigate the landscape and establish home ranges may be more important than natality rates in determining population persistence within the landscape (Fahrig and Paloheimo 1988). Connectivity within a landscape must be maintained or enhanced for populations to stay viable (Fahrig and Merriam 1985). Jones and Garton (1994) speculated that high connectivity of preferred habitats would facilitate the persistence of fisher populations. Our study suggests that forests, which provide overhead cover, are required by fishers for dispersal habitat. Future research should be directed toward quantifying the habitat requirements of fishers during dispersal.

In the landscape in which we conducted our study, the density and dispersion of suitable habitats was sufficient to sustain fishers even though their home ranges included moderate proportions of unsuitable habitat. However, if alteration and fragmentation of late successional forests in our study area continues, the proportion of unsuitable habitat will increase and connectivity among suitable habitats will decrease. Excessive fragmentation and habitat alteration will likely decrease opportunities for acquisition of home ranges by fishers and eventually the landscape will be unable to support a viable population of fishers.

Ecosystem managers should take these factors into consideration when developing landscape-level management plans for fishers. These plans should consider the arrangement and abundance of early seral stages and maintain the connectivity among unfragmented portions of older forest. If ecological processes that occur at the landscape level are retained, it is likely that fisher populations can be maintained in south-central British Columbia.

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FISHER MATERNAL DEN SITES IN CENTRAL NEW ENGLAND

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Abstract: During March-July 1992-1995 we characterized 56 maternal dens and adjacent habitat used by 19 radio-collared adult (≥2 years old) female fishers (*Martes pennanti*) in north-central Massachusetts and southwestern New Hampshire. We compared these characteristics with those of habitat in a small portion of the study area to assess their usefulness to forest managers seeking to maintain or enhance fisher populations. Fishers tended to den in overstory ($P < 0.001$) and understory ($P < 0.001$) cover types dominated by softwoods. Used individual den trees were not different from forest composition ($0.05 < P < 0.10$). Fishers tended to select larger den-tree diameter classes ($P < 0.001$) and dead trees ($0.005 < P < 0.01$). Significantly larger diameter trees ($P = 0.02$), larger den openings ($P = 0.028$), and lower entrance heights ($P = 0.012$) were used later in the season. Fishers often relocated their maternal dens (0-4 times per litter); possible causes of den abandonment and subsequent relocation are discussed. We present a set of guidelines to identify potential fisher maternal den trees so that they can be protected during timber harvesting.

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Introduction

Understanding habitat selection by forest-dwelling wildlife is relevant to formulating and implementing suitable forestry practices to enhance wildlife populations. Certain forestry practices may reduce habitat quality for mammals by removing large diameter trees, stumps, snags, and fallen logs that serve as maternal den sites and resting sites, or provide foraging cover or microhabitats (Masters 1980, Buskirk 1984, Wynne and Sherburne 1984, Spencer 1987). Availability of maternal den sites (repeatedly used sites occupied by an adult female and her kits during the period when the latter are still dependent on the mother for food) has been considered as a potential factor limiting carnivore populations (Schmidt 1943, Bergerud 1969). Sufficient availability of den sites is important because trees may differ in their ability to provide energetic, thermoregulatory, or microclimatic parameters critical to the rearing and survival of the young (Wynne and Sherburne 1984). Habitat loss due to nonselective timber harvesting practices has been implicated in historical fisher (*Martes pennanti*) population declines (Powell 1993). Thus, maternal den sites should be included in any assessment of habitat requirements (Wynne and Sherburne 1984) of fishers and related carnivores.

We located and described maternal den trees and their surrounding habitat in north-central Massachusetts and southwestern New Hampshire to identify important variables for selection of maternal dens by fishers. Our objective was to define characteristics of fisher maternal habitat and den structures so that this information might be used to maintain fisher populations or enhance reproduction. We compared our findings with other studies of maternal dens to determine if the results are broadly applicable to fishers.

Study Area

The study area encompasses approximately 325 km^2 in northern Worcester County in north-central Massachusetts and a small area in southern Cheshire County in southwestern New Hampshire. Topography in the area is moderately steep with elevations of 220-420 m. Forest is interspersed with rural human settlements and one large town (>11,000 inhabitants) is adjacent to the study area.

The area overlaps 2 forest vegetation zones: northern hardwoods-hemlock-white pine and transition hardwoods-white pine-hemlock (Westveld et al. 1956). Dominant hardwoods include northern red oak (*Quercus rubra*), red maple (*Acer rubrum*), American beech (*Fagus grandifolia*), and various birches (*Betula* spp.). Dominant softwoods are white pine (*Pinus strobus*) and eastern hemlock (*Tsuga canadensis*).

Mean temperatures range from 6°C in January to 20°C in July. Mean annual precipitation averages 100 cm (United States Department of Commerce, Environmental Data and Information Service 1982), and mean annual snowfall is 113 cm (National Weather Service, Bloomfield, Connecticut).

Fishers are distributed throughout most continuous forests in Massachusetts and New Hampshire (DeGraaf and Rudis 1986). Density in the main study area averaged about 21 fishers/100 km^2 (York 1996).

Methods

Twenty-two radio-collared adult female fishers were monitored at least 4 times per week from approximately 15 February until 1 June during 1993-1995 to locate maternal dens. Maternal dens were identified by mapping at least 2 consecutive telemetry fixes at the same coordinates, followed by visiting the site on foot to verify that the animal was inside a cavity at that location. At the majority of these sites we either saw (by climbing trees to extract the kits for marking) or heard kits present inside the den, but a few dens were abandoned or relocated before we could observe the occupants. However, the repeated use of these sites (≥3 consecutive fixes in 1 location) for long periods of time, and our failure to detect any repeatedly used, non-maternal resting sites in the vicinity of any confirmed dens, make us confident that all dens we analyzed were indeed maternal dens. Furthermore, Paragi et al. (1996) noted that "use of the same tree cavity on >2 consecutive days by adult (≥2-yr-old) females was assumed to indicate establishment of a natal den and birth of young because other fishers usually did not show this behavior during spring." A few ambiguous sites were nevertheless excluded from the analysis. After 1 May (which we arbitrarily chose as the end of the breeding season), we revisited all maternal den sites, identified the trees to species and measured tree height, diameter at breast height (dbh), and diameter at den-opening height. We also measured den cavity-opening size, aspect, and height above ground, as well as cavity depth. Within a 25-m diameter area centered on the den tree, we visually estimated understory and overstory coverage and recorded species composition, canopy height, and slope aspect.

Initial data analysis revealed no tendency for individual females to repeatedly use den trees or sites with particular characteristics; any given fisher used a wide variety of den types and sites for virtually every variable we examined. Therefore, we used individual dens as our sampling unit and did not group dens used by the same female.

Overall habitat characteristics were estimated in a 6.3-km^2 subunit within the study area (Phillipston Wildlife Management Area). This comparison allowed us to apply our findings to a specific area where forests are maintained for wildlife. Tree data were collected at 155 points in upland forest on a stratified random

10-chain grid (1 point per 4 ha) using a 10-factor wedge prism. Species and dbh were recorded for each tree in the tally. Using a conversion factor where each tree tallied represented 2.29 m^2 of basal area per ha of habitat, the number of trees per ha by diameter class was estimated by dividing 2.29 m^2 by the actual basal area measured at a given sample point. For example, a sampled 36-cm dbh tree consists of approximately 0.1 m^2 of actual basal area, which converts to (2.29 m^2 per ha)/(0.1 m^2 of actual basal area) = 23 trees per ha (Bell and Dilworth 1993).

Percentages of trees in various categories (e.g., live *versus* dead) in the subunit were converted to equivalent numbers of such trees in a sample of the same size as the number of fisher dens examined. Then, for each variable examined (e.g., number of sites consisting of a given overstory species, stand type, dbh category), a chi-square test for homogeneity was performed to compare actual den site use by fishers with site composition in the subunit (Marcum and Loftsgaarden 1980, Thomas and Taylor 1990). Categories were pooled in some comparisons to ensure that ≤20% of the contingency table cells had expected frequencies <5 and that no cell had an expected frequency <1 (Cochran 1954).

The proportion of the total number of trees sampled that were less than 80% sound and contained visible cavities was also determined for the 6.3-km^2 subunit to estimate the number of potential den trees in a typical female's home range (7-8 km^2, York 1996). However, this estimate does not consider opening height, entrance size, or habitat type. Furthermore, degree of soundness may be difficult to estimate in trees with no externally visible cavities. Thus, any calculation of the number of potential den trees is likely an underestimate with respect to degree of soundness, but an overestimate with respect to trees with suitable entrance-opening measurements.

Results

Fifty-six maternal dens were used by 19 fishers (3 of the 22 females monitored did not den). Not all variables could be measured for a few den trees, so sample sizes are smaller for a few comparisons. Since some females were tracked for more than 1 year of the study, the monitoring of these 19 females consisted of 30 "fisher-seasons" (Paragi 1990). All dens were in tree cavities. Estimated parturition dates for 20 litters ranged from 4 March to 24 March (median = 17 March). Initial maternal dens (i.e., natal dens) were occupied for an estimated 10 to 59 days (median = 27, $\bar{x}$ = 28.7, SD = 14.3, n = 18). Fishers used 1-5 maternal dens (median = 2) between parturition and 3 June; after that time they made increasing use of temporary dens (cavities or nests used for only a day or 2 at a time) as the kits became larger and more mobile. Distances between consecutive dens ranged from 47 to 1820 m (median = 475, $\bar{x}$ = 569, SD = 396, n = 33).

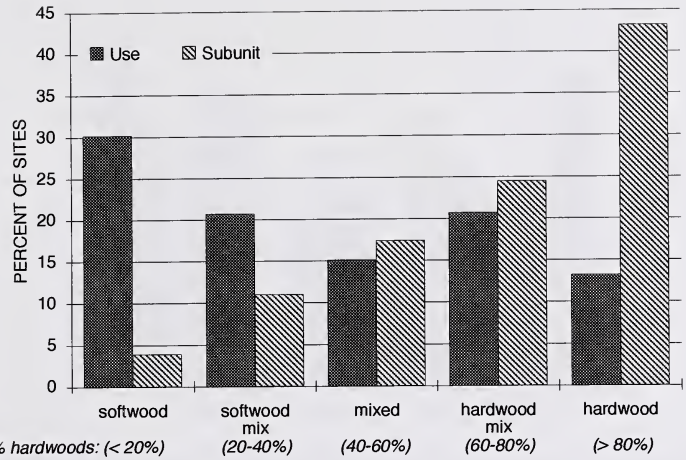

Figure 1. Overstory cover types at fisher (*Martes pennanti*) maternal den sites (n = 53) in north-central Massachusetts and southwestern New Hampshire, 1993-1995, compared with types present in a 6.3-km^2 subunit of the same study area.

Maternal dens were located more often in softwood overstory and less often in hardwood overstory in the study area when compared with the relative proportions of these overstory types in the subunit ($\chi^2 = 21.04$, 4 df, $P < 0.001$; Fig. 1). Sites where eastern hemlock is the dominant overstory species were used more and sites where maples (*Acer* spp.) are the dominant overstory species were used less than their proportions in the subunit ($\chi^2 = 13.04$, 4 df, $0.01 < P < 0.025$; Fig. 2). In addition, softwood understory was used more commonly than hardwood understory when compared with the subunit ($\chi^2 = 18.77$, 2 df, $P < 0.001$). Sites where red maple is the dominant understory species were used less, and sites where hemlock is the dominant understory species were used more, than their proportions in the subunit ($\chi^2 = 40.70$, 3 df, $P < 0.001$).

White pine and eastern hemlock together accounted for approximately 60% (n = 32) of fisher den trees, but species were used as den trees in the study area in proportion to the relative occurrence of these species in the subunit ($\chi^2 = 9.81$, 5 df, $0.05 < P < 0.10$; Fig. 3). The following tree species were used as maternal dens (in descending order): white pine (*Pinus strobus*), eastern hemlock (*Tsuga canadensis*), northern red oak (*Quercus rubra*), red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), shagbark hickory

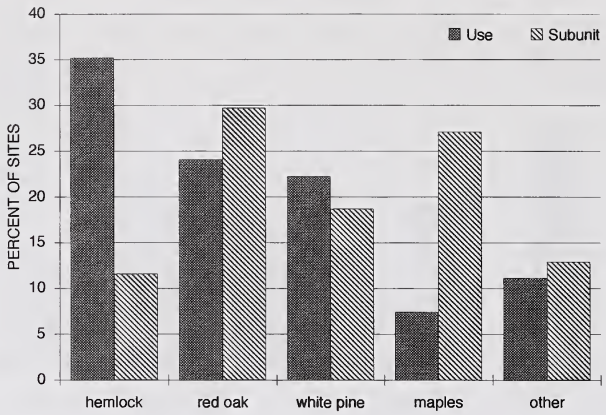

Figure 2. Dominant overstory species at sites used by fishers (*Martes pennanti*) for maternal den sites ($n = 54$) in north-central Massachusetts and southwestern New Hampshire, 1993-1995, compared with dominant species in a 6.3-km^2 subunit of the study area.

(*Carya ovata*), black birch (*Betula lenta*), white ash (*Fraxinus americana*), and American basswood (*Tilia americana*). Dead trees (snags) constituted 19% of den trees, but only 2% of subunit trees ($\chi^2 = 7.72$, 1 df, $0.005 < P < 0.01$). Den trees also had significantly greater dbh measurements than did subunit trees ($\chi^2 = 39.70$, 3 df, $P < 0.01$; Fig. 4).

Statistical conclusions for habitat variables did not change when dens from the latter part of the denning season were excluded. However, den tree measurements (Table 1) differed during the year. After 1 May, fishers used larger dbh trees for maternal dens ($U = 161$, $P = 0.02$, Mann-Whitney test), den openings were larger ($U = 139$, $P = 0.028$, 1 extreme outlier deleted), and heights of den openings above ground were lower ($U = 379$, $P = 0.012$) (Table 2). There was no significant change in the internal depth of the den cavities after 1 May ($U = 255$, $P = 0.855$). Both den-opening aspect ($z = 0.55$, $P > 0.50$) and slope aspect ($z = 0.50$, $P > 0.50$) were uniformly distributed with respect to compass direction (Rayleigh test, Zar 1984).

Assuming that the trees we identified were representative of maternal dens used by fishers, of the estimated 40,000 trees per female fisher's home range in the subunit, approximately 1000 (2.4%) were less than 85% sound with visible cavities, making them potential maternal den trees.

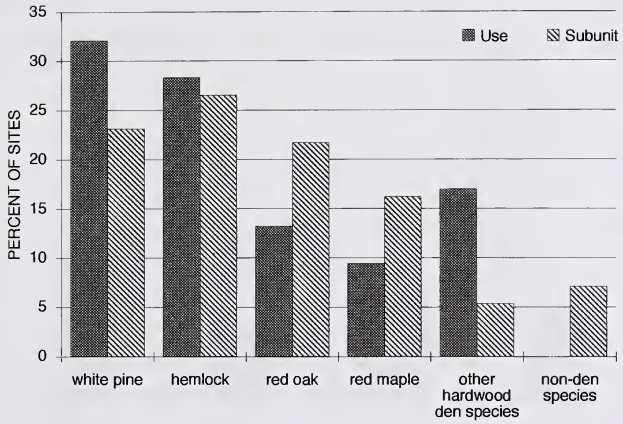

Figure 3. Use of various tree species as fisher (*Martes pennanti*) maternal den sites (n = 53) in north-central Massachusetts and southwestern New Hampshire, 1993-1995, compared with species present in a 6.3-km^2 subunit of the study area.

Discussion

Paragi et al. (1996) provided data on 33 fisher maternal dens in south-central Maine; other studies have observed no more than 5 individual dens (Grinnell et al. 1937; Hamilton and Cook 1955; Kelly 1977; Leonard 1980, 1986; Mullis 1985; Roy 1991; Kohn et al. 1993). Paragi et al. (1996) reported disproportionately greater use of sites in hardwood and scrub overstory types for maternal dens than of mixed forest sites in Maine; use of softwood sites was not different from that of other overstory types. These findings differ from ours and likely result from differing forest compositions between the two areas.

The species or type (hardwood *versus* softwood) of tree used as a maternal den site was relatively unimportant compared with the other variables measured. Although we found that the majority of den trees were white pine or eastern hemlock, these species, or softwoods in general, were not used disproportionately more often. Furthermore, Paragi et al. (1996) reported that the majority of maternal dens (94%) in Maine were in hardwoods.

The apparent selection of dead trees for maternal dens in our study area parallels the findings of Paragi et al. (1996); 50% of their maternal fisher dens were in dead trees. Dead trees may be more likely than live trees to contain large cavities

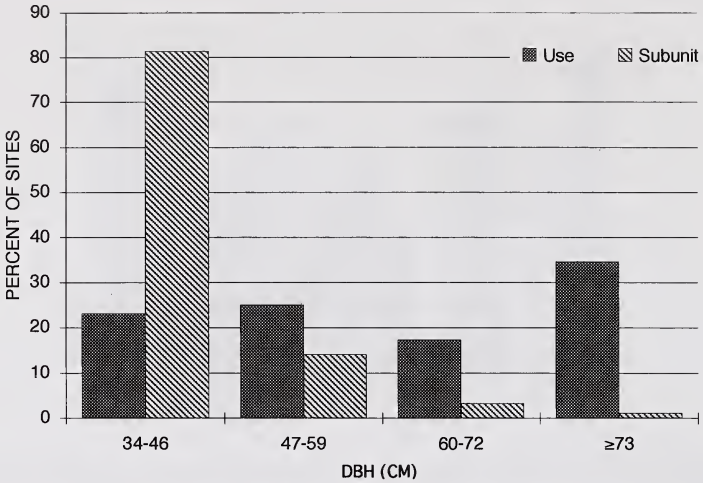

Figure 4. Trees of various diameter at breast height (dbh) used by fishers (*Martes pennanti*) as maternal den sites (n = 52) in north-central Massachusetts and southwestern New Hampshire, 1993-1995, compared with dbh classes present in a 6.3-km^2 subunit of the study area.

resulting from rotting wood. The large number of live trees used for maternal dens in both studies is likely a result of the much larger availability of live trees (e.g., roughly 97% in our study area) than dead trees. Many live trees contain natural cavities caused by disease, some of which are enlarged by other animals such as woodpeckers (Picidae) (Conner et al. 1976, Miller et al. 1979).

Paragi et al. (1996) found that fishers used considerably smaller dbh trees for maternal dens than our fishers did; perhaps absolute size of den trees is less important than their relative size compared with other available trees in a particular area. Larger maternal den trees are probably used later in the denning period to accommodate the growth of the kits.

The sizes of the maternal den openings in our study area were comparable to those of Paragi et al. (1996), as was the finding that openings were significantly larger in later dens than in earlier dens (not statistically significant in their study). Small openings may be important for excluding potential predators when the kits are relatively defenseless, whereas larger openings may facilitate the removal of larger kits when changing den sites. Larger openings may also provide better heat dissipation or ventilation as the weather becomes warmer.

Table 1. Characteristics of cavity trees used by fishers (*Martes pennanti*) for maternal dens in north-central Massachusetts and southwestern New Hampshire, 1993-1995.

				Opening[c]		
	dbh[a]	Height above ground[b]	ddh[b]	Length	Width	Area
Range	36-127	1.90-15.40	30-104	8-99	5-23	47-1788
Median	60	6.00	48	16	8	94
$\bar{x}$	66	6.28	53	22	9	164
SD	24	2.70	18	17	3	250
n	52	51	51	50	51	50

[a] Diameter at breast height (cm).

[b] Height of den opening above ground (m), and diameter of tree (cm) at this den opening height (ddh).

[c] Length (cm), width (cm), and area (cm^2) of opening to den. Area was estimated as ($\pi \times$ length $\times$ width)/4 (Paragi et al. 1996).

Our finding that fishers selected tree cavities for all of their maternal dens is supported by observations from other investigators in the northeast (Hamilton and Cook 1955, Kelly 1977, Paragi et al. 1996), and in other regions (Leonard 1980, Mullis 1985), but there have been reports of maternal dens in a rock outcrop (Grinnell et al. 1937) and in a downed hollow log (Roy 1991). The entrance heights we measured in our study area are very similar to those found by Paragi et al. (1996), suggesting that fishers preferentially select for den entrances above ground level. Elevated den entrances may be another means of excluding ground-dwelling predators (Leonard 1980) and meeting thermoregulatory needs (Raine 1981, Buskirk 1984, Wynne and Sherburne 1984, Walsberg 1985, Buskirk et al. 1989). Kilpatrick and Rego (1994) believed that tree cavities provide fishers with a less severe microclimate than other types of resting sites in winter, and Geiger (1965) determined that elevated areas remain warm longer than ground-level areas during spring. Our observation that den-opening heights were significantly lower after 1 May might reflect the warmer temperatures at that time of the year, or the decreased risk of predation as the kits become older. Alternatively, the larger diameter of tree trunks closer to the ground may provide larger cavities; den openings may therefore be closer to the ground simply because growing fisher kits need the larger cavities that may be found there.

The frequent changing of maternal den sites observed by us and Paragi et al. (1996) reinforces the importance of managing habitat (i.e., individual trees) to provide an adequate number of alternative den sites from which fishers can

Table 2. Comparison of den tree measurements at fisher (*Martes pennanti*) maternal den sites based on date of first occupation in north-central Massachusetts and southwestern New Hampshire, 1993-1995.

				Cavity opening[c]								
	dbh[a,b]			Height[b]			Area[b]			Cavity depth[d]		
	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*
Before 1 May	63	4	32	7.05	0.53	31	102	10	31	98	12	31
After 1 May	76	5	17	5.11	0.34	17	276	105	16	114	28	17

[a] Diameter at breast height (cm).

[b] Means are significantly different (see text).

[c] Height above ground (m) and area (cm^2) of opening to cavity. Area was estimated as ($\pi \times$ length $\times$ width)/4 (Paragi et al. 1996).

[d] Means are not significantly different (see text).

choose. We considered 5 possible causes for litter relocation in fishers. First, fishers may be avoiding parasites (Young 1951, Andrews and Bogess 1978) or wastes. Many of the abandoned dens we examined were heavily infested with fleas, and a few den trees we examined contained many scats or remnants of prey items (cf. Roy 1991). However, most dens were very clean, with little evidence of use (cf. Hodgson 1937; Leonard 1980, 1986). Second, fishers may prefer to relocate surviving kits rather than remove a dead kit from the den. One of our dens in which such an abandonment occurred was later reused by the same litter after we removed the dead kit, suggesting that the presence of the dead kit was the main cause of abandonment. Third, kits may outgrow certain dens (see above). Fourth, fishers may move their litters to provide easier access to food sources, such as white-tailed deer (*Odocoileus virginianus*) and raccoon (*Procyon lotor*) remains (Powell et al., this volume), in order to reduce the amount of time they need to leave the kits unattended while they forage. Fifth, disturbance by a potential predator or by human activity may cause fishers to relocate litters. Paragi et al. (1996) felt that their disturbance of the dens may have induced more frequent den relocation. Our fishers also relocated to other dens after we handled kits, regardless of whether the mother was present at the time the den was disturbed. However, noting that later-used dens are even more accessible to predators (i.e., lower entrance heights, larger entrance sizes), factors other than disturbance may also contribute to relocation. Furthermore, fishers in our study did not appear to be overly affected by nearby human activity. On a few occasions we found maternal dens within only a few meters of maintained or actively utilized roads, and on 1 occasion timber harvesters were felling

trees within 5 meters of an active den, but this activity did not induce abandonment of the den site by the fisher (cf. Johnson and Todd 1985).

Management Implications

It has been stated that "habitat is the main concern involving . . . the fisher today" (Buskirk 1992:318), and habitat loss due to logging has been a major factor blamed for historical declines of fisher populations (Powell 1993). It has been suggested that fisher habitat management be performed on a landscape scale (Harris 1984, Jones and Garton 1994). In addition, however, we recommend that finer-scale management practices be considered to augment habitat characteristics important for fisher reproduction. We acknowledge that larger-scale habitat variables such as canopy closure and composition must also be considered in managing fisher habitat, since a potentially ideal den tree may not be used by fishers if the surrounding habitat is unsuitable.

We recommend that timber harvesters employ the guidelines of den identification (Table 1) to preserve trees with possible fisher maternal dens. Emphasis should be placed on preserving dead and decaying trees, not only because they are selectively utilized by fishers, but because they provide feeding and shelter sites for many other animals (Thomas et al. 1979). Healy et al. (1989) demonstrated for a study site near our study area that preservation of cavity trees could be accomplished with little impact on timber yields, because 96% of harvestable trees, 89% of rough cull trees, and 63% of rotten cull trees in their study area did not contain cavities. They also found that the majority (conservatively estimated at 63%, but potentially more during the breeding season) of all cavities observed were being used by some bird or mammal, underscoring the importance of preserving such trees even if enhancing fisher reproduction is not a priority.

Current US Occupational Safety and Health Administration (OSHA) regulations require removal of dead or decaying trees (termed "danger trees") during logging occupations (29 CFR Ch. XVII §1910.266(h)(1)(vi)). We recommend that these regulations be relaxed in the interest of forest stewardship, perhaps by exempting potential den trees from the rule.

The large number of potential maternal den trees we observed in a typical home range of a female fisher in central New England indicates that fisher reproduction in this region is presently not limited by the availability of den sites. However, in areas where fisher habitat is less suitable, or where timber harvesting pressures are more intense, fisher reproduction may be compromised by an inadequate number of potential den sites. In any region where enhancement of fisher populations is a priority, suitable forest management practices can foster the reproductive success of the fisher.

Acknowledgments

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SEASONAL FOOD HABITS OF FISHERS IN CENTRAL NEW ENGLAND

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Abstract: During 1992-1994, we compared food habits among seasons of fishers (*Martes pennanti*) in Massachusetts and New Hampshire by identifying remains in scats ($n = 169$), gastrointestinal tracts ($n = 57$) and uneaten prey remains (orts, $n = 34$). Forty-four food types were identified, and significant differences ($P < 0.05$) were evident among niche-breadth indices from different seasons. Although mammalian prey (chiefly eastern gray squirrel, *Sciurus carolinensis,* and raccoon, *Procyon lotor*) was the most prevalent food, fruits were important in some seasons. Gray squirrels were eaten more by females than by males ($P = 0.006$), and raccoons were eaten more by <1-year-olds than by >1-year-olds ($P = 0.002$). We also noted a high prevalence of raccoons in the fisher diet in towns where rabies had recently become established in raccoons. The high diversity in fisher diets in our study suggests that fishers are opportunistic foragers, and that they may diversify their diet when preferred food types are scarse seasonally, episodically, or geographically.

Introduction

Food habits of mammalian carnivores are often studied by examining scats, stomachs and intestines (gastrointestinal [GI] tracts), or uneaten prey remains (orts). However, many dietary studies fail to account for seasonal differences in a predator's diet. This deficiency can lead to spurious conclusions because availability of prey species may vary throughout the year; thus, comparisons of different predator dietary studies for a given species may not be valid if the data come from

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different times of year (Litvaitis et al. 1994). Comparisons among different seasons, however, can be important in revealing a predator's flexibility in using alternative food sources that periodically or geographically change in their relative abundance.

Fisher (*Martes pennanti*) food habits have been studied across North America (see Powell 1993 and Martin 1994 for references). However, few seasonal comparisons (Coulter 1966, Clem 1977) have been attempted for fishers or other mustelids (Moors 1980), and to our knowledge no studies involving year-round sampling of food habits exist. In this study we examined scats, GI tracts, and orts from fishers in Massachusetts and southwestern New Hampshire to assess seasonal, sex-related, and age-related differences in diet. We also compared 3 niche-breadth indices (measures of diet diversity) used in studies of food habits, and investigated a possible relationship between a recent rabies epidemic in the study area and the observed high incidence of raccoons (*Procyon lotor*) in the diet of fishers in Massachusetts.

Study Area

Most of the scats were collected in an approximately 210-km^2 area in northern Worcester County in north-central Massachusetts. A few scats were collected from adjacent Cheshire County in southwestern New Hampshire, and several of the scats and GI tracts were collected (or provided by trappers) from other towns in the fisher's range in Massachusetts. All food samples were collected within a 93-km radius of the center of the main study area. The study area and habitat are described in Powell et al. (this volume).

Methods

Sources of Food Samples

Scats were collected from trap sites (either from immobilized fishers, or in or near traps), resting sites, maternal den sites (Powell et al., this volume), camera stations (York 1996), during snow tracking, while handling tranquilizer-darted fishers, and along trails or roads between October 1992 and October 1994. Many of the scats were from cage-trapped or radio-tracked fishers ($n = 92$ individuals) whose ages were estimated from counts of cementum annuli of extracted upper first premolars (Strickland et al. 1982). The GI tracts were collected from trapper-provided carcasses (trapped primarily in cage traps) during the November 1 to 22, 1992, trapping season. Scats and GI tracts were frozen until analyzed. Orts were found at resting sites, maternal den sites, and while snow tracking. Two reliable reports of observed kills were recorded by residents. Ort and observed kill data were collected for descriptive purposes only and were not used in any statistical comparisons or niche-breadth calculations.

Laboratory Analysis of Food Samples

We followed the procedures outlined in Webb (1976) and Kennedy and Carbyn (1981) for initial preparation of the scats and hair samples. Thawed scats were washed in a 0.62-mm sieve, and microscopic fractions were discarded. Dried scat contents were examined under a binocular dissecting microscope, and a visual estimate (e.g., Grenfell and Fasenfest 1979, Wise et al. 1981, Saunders et al. 1993) of the percentage by volume of each food item was recorded. A subsample of the scats was reevaluated by an independent observer, whose estimates differed by <10%. Mammalian guard hairs were identified by a combination of macroscopic and microscopic characteristics, including coloration, banding patterns, diameter (measured with an ocular micrometer in a 40-100 power compound binocular microscope), medulla configuration (examined using Permount®-mounted hairs [Fisher Scientific, Fair Lawn, New Jersey]), and cuticular scale characteristics, using several keys (Mayer 1952, Stains 1958, Adorjan and Kolenosky 1969, Moore et al. 1974). Reference guides were used to identify mammal teeth and bones (Brainerd 1939, Stains 1959, Olsen 1964, Hillson 1986, Gilbert 1990), bird feathers (identified to order, when possible; Day 1966, Kennedy and Carbyn 1981), and plant seeds (Montgomery 1977). Plant seeds and mammal remains (bones, teeth, and hairs) were also compared with museum reference specimens.

The GI tracts were dissected to remove their contents. Some consisted of only the stomach, whereas others had the intestine attached. In the latter case, stomach and intestine contents were examined separately. In almost all cases, either the stomach or the intestine was empty. In the 4 GI tracts in which both the stomach and the intestine contained food, 2 contained only trap bait or plant debris, and were not counted, 1 contained bait in the stomach, and only the intestine was counted, and 1 contained the same prey items in nearly equal proportions in the stomach and intestine. In the last instance the 2 samples were averaged and treated as a single sample. Because the indigestible parts of food items that formed the basis for scoring were similar in stomachs and intestines, no distinction was made between the 2 (Hamilton 1959, Day 1968, Akande 1972, Korpimaki and Norrdahl 1987). The GI-tract contents were often examined directly without prior washing, and data were recorded as estimates of indigestible parts of the food bolus that would be present in a washed scat. We assumed scats and GI tracts to be comparable in the analyses that follow (Coulter 1966, Powell 1993) because we made an effort to collect only fresh and intact scats, and because the types of remains used for the aggregate percent calculations were hairs, teeth, bones, and seeds, which showed no appreciable weathering in the field or noticeable alteration by digestion (cf. Williams 1938, Williamson 1951, Short 1978). Indigestible food items in GI tracts were identified in the same manner as for scats.

Plant debris (other than fruit) was considered to have been eaten incidentally or to have been ingested as fishers attempted to escape from cage traps (Coulter 1966, Rego 1984, Reynolds and Aebischer 1991), and was not included in the data analyses (Latham 1950). Similarly, fisher hair in most food samples was considered the result of grooming (Jones 1991) or escape attempts (Hamilton 1959), and was tabulated as a separate non-food trace item unless it composed > 3% of the estimated volume of an average-sized scat. Trace items (<0.5% of the volume of all other food types) were included in percent occurrence data, but were assigned a volumetric percentage of 1×10^{-10}%, making the calculations involving logarithms possible and effectively ignoring them in the aggregate percent calculations. We identified items known or suspected to be bait by considering commonly used fisher baits (de Vos 1952, Kelly 1977, Brown and Will 1979, Giuliano et al. 1989) and by comparing our food samples from trapped *versus* non-trapped fishers; these items were excluded from the analyses (Day and Linn 1972, Reynolds and Aebischer 1991).

Food items were identified and classified to the most specific level possible (Greene and Jaksic 1983), with the following exceptions. Fruits were combined into a single category to facilitate comparisons with Martin's (1994) fisher food diversity indices. Small murid rodent (mice and voles) remains were similarly combined, which allowed the inclusion of a number of unidentified small rodents in the data analyses. We combined birds for the same reasons, and because identification to species level was often impossible (Dunstone 1993). Unidentified foods were placed in broad categories (e.g., fruits) where possible, or were excluded from the analyses (we assumed that these unidentified items represented unidentifiable portions of previously identified food species, rather than new food types [Clem 1977, Reynolds and Aebischer 1991, Martin 1994]).

Data Analysis

Percent occurrence (proportion of the total number of scats or GI tracts containing a given food type) calculations are presented for ease of comparison with other studies, and for comparisons where the frequency of taking prey was of greater interest than their relative volume in the diet. Percent occurrence was not used in the seasonal, age, and sex comparisons because this measure tends to overestimate the importance of small prey in terms of weight, and underestimate them in terms of numbers, as compared with larger prey (e.g., Lockie 1959, Rosenzweig 1966, Mech 1970, Floyd et al. 1978). In addition, percent occurrence is arguably appropriate only if the majority of the stomachs in a sample contain only a single prey type (King 1980, Erlinge 1981, Wallace 1981, Ackerman et al. 1984). Although the aggregate percent method presents similar problems, we believe that the use of a method that estimates the relative bulk of prey items provides a more accurate representation of the relative quantity of

each type of prey consumed than a method that simply records presence or absence of a prey item. Aggregate percent (the percentage by volume of a given item in a scat or GI tract, averaged across all food samples) was therefore used for all statistical analyses and niche-breadth calculations. Percentages sum to 100% even if individual food samples contain multiple prey types, and this method allowed the direct comparison of scats and GI tracts because each food sample was weighted equally (e.g., Martin et al. 1946, Larimore 1957, Swanson et al. 1974, Wallace 1981).

Only food samples for which the season was known were used in niche-breadth calculations. Adjusted sample sizes were calculated after removing bait, plant debris, and unidentifiable items from the original data, so that the totals of the aggregate percentages for identifiable food types would equal 100%.

For a subset of the food samples, sex (n = 156) or age (n = 154) was known with reasonable certainty, as determined by collecting scats from trapped or darted fishers, or from occupied resting sites or maternal den sites. For these samples, we compared the occurrence of the 6 most prevalent food types between age groups (juveniles [age 4-12 months] *versus* adults [age >1 year]) and sexes using randomization tests with 1000 replications (Manly 1990). Conventional chi-square or similar tests were not used because, after dividing the diet into multiple categories and removing non-food items from the sample, too many of the contingency table cells had expected frequencies of <5 (Cochran 1954), and because food categories were not mutually exclusive (a given fisher scat often contained more than 1 type of food). The randomization approach circumvented these limitations. We initially attempted to partition the different variables being compared (e.g., to keep age groups and seasons separate when comparing sexes), but this subdivision of the data resulted in sample sizes that were too small to test statistically and produced anomalous results in the randomization tests. We therefore tested 1 variable at a time and believe that the randomization procedure thoroughly homogenized the data with respect to the other variables. When testing for age differences in the diet, we only considered data from the summer, early autumn, and deer-hunting seasons, because there were very few food samples collected from juveniles in either winter or spring. Significance levels were calculated using the Bonferroni adjustment for multiple simultaneous comparisons, with $\alpha = 0.05/6 = 0.0083$.

We defined 5 seasons based on biological considerations (Larimore 1957, Coulter 1966). We defined winter (January to March) by the presence of snow cover, which was expected to reduce availability of small rodents and increase abundance of deer carrion. Spring (April to May) was characterized by the disappearance of snow cover and the migration and beginning of nesting by birds. Spring is also a time of high energy demands on lactating adult female fishers. Summer (June to August) was characterized by the widespread availability of

certain fruits, such as blueberries (*Vaccinium* spp.), black cherries (*Prunus serotina*), and serviceberries (*Amelanchier* spp.). Early autumn (September to October) was characterized by large numbers of migrating birds (Coulter 1966), and larger small mammal populations because of summer recruitment. The late autumn deer-hunting season (November to December) was expected to provide abundant carrion in the form of entrails of field-dressed deer (deer-hunting seasons in Massachusetts were 7 November to 21 December), and was distinguishable from winter by lack of appreciable snow cover.

We calculated niche-breadth indices to compare the diversity of fisher diets among seasons based on aggregate percent values (Bethke 1991). We compared the Levins index (B, Levins 1968), the Shannon index (H', Shannon and Weaver 1963) and the Brillouin index (H, Brillouin 1960) for each of the 5 seasons. To avoid sample-size biases, repeated random samples of equal size (subsample n = 14) were drawn from a larger sample of 211 scats and GI tracts of known season (Brower et al. 1990). Niche-breadth indices are the averages of 25 subsamples from each season. A nonparametric Tukey-type multiple comparison test was then performed on the mean Brillouin values (Zar 1984).

The relationship between the recent rabies outbreak in Massachusetts and the prevalence of raccoons in the fisher diet was examined by separately calculating the relative frequency of raccoons in the fisher diet (the number of occurrences of raccoon as a percentage of the total number of different prey items in all food samples) for food samples collected from 3 types of localities: (1) towns where rabies had not been reported at the time the sample was collected, (2) towns where rabies had first been reported in the year the sample was collected, and (3) towns where rabies had first been reported before the year in which the sample was collected. Rabies incidence was determined from data provided by the Massachusetts Division of Fisheries and Wildlife (MDFW). We recognize that there may be problems with the calendar-year reporting scheme used by the state (e.g., rabies may have been present in a locality long before it was first reported), so our rabies occurrence data should be considered with some caution.

Results

General Food Habits

We collected 169 scats from cage-trap sites (n = 47), resting sites (n = 39), maternal dens (n = 37), snow-tracking sites (n = 14), tranquilizer-darted fishers (n = 9), camera stations (n = 8), and trails or roads (n = 8). Collection site was not recorded for 7 scats. Fifty-seven GI tracts were provided by trappers. Forty specific or mutually exclusive food types were recognized in the scats and GI tracts (Table 1). An additional 4 prey types were identified from orts (n = 35, Table 2) for a total of 44 food types. The cumulative number of food types was

Table 1. Occurrence of food items in 57 gastrointestinal (GI) tracts and 154 known-season scats of fishers in Massachusetts and southwestern New Hampshire during winter (W, $n = 22$), spring (Sp, $n = 52$), summer (Su, $n = 30$), early autumn (EA, $n = 48$), and deer-hunting (DH, $n = 59$) seasons, 1992-1994.

Food type	Aggregate percent[a]						Percent occurrence[b]					
	W	Sp	Su	EA	DH[c]	Year[d]	W	Sp	Su	EA	DH[c]	Year[d]
Small murids		9	5	7	6	5		13	10	15	22	10
Red-backed vole (*Clethrionomys gapperi*)		5	2	1	3	2		8	7	4	5	5
Pine vole (*Microtus pinetorum*)		2				tr		2				tr
Unidentified *Microtus* spp.				2		tr				2		tr
Unidentified microtine		2		3		1		2		6		1
Unidentified cricetid					4	1					5	1
White-footed mouse (*Peromyscus leucopus*)		tr	3			1		2	3			1
Meadow jumping mouse (*Zapus hudsonius*)				2		tr				2		tr
Muskrat (*Ondatra zibethicus*)		tr				tr		2				tr
Beaver (*Castor canadensis*)	3					1	5					1
Porcupine (*Erethizon dorsatum*)	tr	1	tr	tr	6	1	5	8	7	6	10	7
Eastern gray squirrel (*Sciurus carolinensis*)	19	10	18	3	1	12	32	10	33	4	3	19

Table 1 Continued.

Food type	Aggregate percent[a]						Percent occurrence[b]					
	W	Sp	Su	EA	DH[c]	Year[d]	W	Sp	Su	EA	DH[c]	Year[d]
Red squirrel (*Tamiasciurus hudsonicus*)				6		1				8		1
Southern flying squirrel (*Glaucomys volans*)	1	2	tr			1	5	2	3			2
Eastern chipmunk (*Tamias striatus*)		6	tr	tr		1		10	3	2		3
Woodchuck (*Marmota monax*)		tr				tr		2				tr
Unidentified sciurid			tr	2	2	1			3	2	2	1
Unidentified rodent		4		tr	2	1		8		2	5	2
Shrews (*Sorex* spp.)				1		tr				2		tr
Star-nosed mole (*Condylura cristata*)					2	tr					2	tr
Snowshoe hare (*Lepus americanus*)	2	1			4	1	5	4		2	5	3
Eastern cottontail (*Sylvilagus floridanus*)	9		tr	2		3	9		3	2		3
Raccoon (*Procyon lotor*)	13	20		tr	8	8	23	25		2	8	12
Fisher[e]	5				5	2	5				7	2
Striped skunk (*Mephitis mephitis*)					1	tr					2	tr

Table 1 Continued.

Food type	Aggregate percent[a]						Percent occurrence[b]					
	W	Sp	Su	EA	DH[c]	Year[d]	W	Sp	Su	EA	DH[c]	Year[d]
Domestic cat (*Felis catus*)		4		tr	3	1		4		2	7	2
Domestic dog (*Canis familiaris*)		tr				tr		2				tr
Gray fox (*Urocyon cinereoargenteus*)					2	tr					2	tr
Opossum (*Didelphis virginiana*)		5		4	1	2		8		6	2	3
White-tailed deer (*Odocoileus virginianus*)	8	5			tr	3	9	12			5	5
Unidentified mammal	10	4	1	tr	8	5	27	12	10	10	12	15
Birds		7	8	tr	4	4		17	17	4	14	10
Passeriformes		2	2	tr	3	1		6	3	2	7	3
Falconiformes		tr	3	tr	tr	1		2	3	2	2	2
Unidentified bird		5	3		1	2		10	10		5	5
Eggs		tr				tr		2				tr
Snakes[f]	2				tr	tr	9				2	3
Insects[e]		2	2	6	tr	2		6	17	29	2	10
Fruits	1		61	30	4	21	5		83	60	10	34
Prunus serotina			19	10		6			23	19		9
Amelanchier spp.			17			4			30			8

Table 1 Continued.

Food type	Aggregate percent[a]						Percent occurrence[b]					
	W	Sp	Su	EA	DH[c]	Year[d]	W	Sp	Su	EA	DH[c]	Year[d]
Vaccinium spp.		tr	20			5		2	27			7
Rubus spp.			3			1			3			1
Ilex verticillata				8	1	2				10	2	2
Vitis spp.				6	1	1				17	2	3
Sorbus americana				5		1				10		2
Pyrus spp.					2	1					5	1
Viburnum acerifolium	1					tr	5					1
Symphoricarpus albus			2			tr			3			1
Lonicera spp.					tr	tr					3	1
Unidentified plant seeds				1	tr	tr				4	3	1
Plant fibers/debris[g]	4	17	5	23	23	13	5	33	17	44	44	25
Unidentified material	5			tr	1	1	5			2	2	2
Bait[h]	18	2		14	16	10	18	4		38	24	15
Fisher hair (trace)[i]	tr	tr	tr	tr	tr	tr	14	29	23	35	46	28
Insect (trace)[j]		tr	tr	tr		tr		2	3	4		2

[a] Estimated percent by volume of a food type in a given scat or GI tract, averaged across all food samples. For statistical analyses, these values were recalculated omitting bait, plant debris, and unidentified food types. Items <0.5% are listed as "trace" (tr).

[b] Percentage of the total number of food samples examined that contained a given food type, including trace occurrences. Items <0.5% are listed as "trace" (tr).

[c] All 57 GI tracts and 2 of the scats were collected in this season.

Table 1 Continued.

[d] Weighted year-round average.
[e] As a major constituent of the food sample (presumably a prey item).
[f] Probably *Thamnophis* spp.
[g] Assumed to be ingested incidentally, or eaten as fishers attempted to escape from trap.
[h] Includes beaver, muskrat, chicken, fish, and other items which were known or suspected to have been used as bait for a particular food sample.
[i] Fisher hair was tabulated separately as a non-food trace occurrence when it composed <3% of the estimated volume of an average-sized scat or GI tract, and was presumed to result from grooming.
[j] Trace occurrences of insects were presumed to have been eaten incidentally, or to have been present inside the stomach of a larger prey, or to have been living on the scat at the time of collection.

Table 2. Prey remains (orts) and witnessed kills by fishers in Massachusetts and southwestern New Hampshire, 1993-1995.

Prey species	Season	Number of occurrences
Mammals		27
White-tailed deer	Winter	3[a]
	Spring	1[a]
	Deer-hunting	6[b]
Eastern gray squirrel	Winter	1[a]
	Spring	3[c]
Red squirrel	Spring	2[d]
Eastern chipmunk	Spring	2[d]
Domestic cat	Winter	1[a]
	Unknown	1[e]
Raccoon	Winter	1[f]
	Unknown	1[g]
Porcupine	Spring	1[d]
Beaver	Winter	1[a]
Red-backed vole	Spring	1[d]
Star-nosed mole	Spring	1[d]
Snowshoe hare	Winter	1[a]
Birds		7
Wild turkey[i] (*Meleagris gallopavo*)	Spring	2[h]
	Deer-hunting	1[f]
Ruffed grouse[i] (*Bonasa umbellus*)	Spring	1[d]
Domestic goose[i] (*Anser domesticus*)	Winter	1[f]
Hairy woodpecker[i] (*Picoides villosus*)	Spring	1[d]
Unidentified bird	Spring	1[f]
Total		34

[a] Orts found during snow tracking.
[b] Assumed to be entrails of field-dressed deer left by hunters.
[c] Includes 2 orts found at a fisher maternal den site and 1 ort found at a fisher resting site.
[d] Orts found at fisher maternal den sites.
[e] Fisher reported carrying away a freshly killed cat.
[f] Orts found at fisher resting sites.
[g] Fisher reported killing a raccoon.
[h] Includes 1 ort found at a maternal den site and 1 ort found at a resting site and later carried by the fisher to a nearby maternal den site.
[i] Items not identified at species level in scats or GI tracts.

plotted against the number of food samples (drawn in random order) examined. This plot revealed that the maximum species richness of the sample was attained after examining approximately 75% of the food samples, suggesting that our sample was more than sufficient to enumerate the typical food types in the fisher diet.

Mammals and fruits, in that order, were the 2 most prevalent broad food classes, followed by birds, insects, and reptiles. Seven food types were found to be either seasonally or broadly prevalent (either >5% aggregate percent overall, or >13% in any 1 season) in the fisher diet (Fig. 1); subsequent analyses were based on these major food types. White-tailed deer were not included in the age or sex comparisons because deer was not adequately represented in the subsamples examined. The other 6 food types were sufficiently represented in the subsamples to make valid comparisons between age and sex groups.

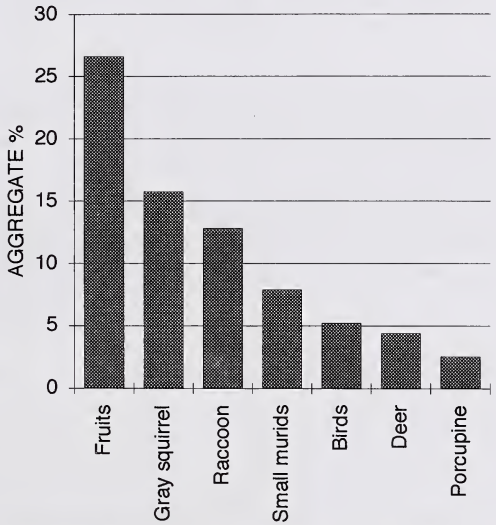

Figure 1. Aggregate percentages of the 7 major food groups in the diet of fishers in Massachusetts, 1992-1994. Data are from scats (n = 154) and GI tracts (n = 57), and are average percentages of estimated volume of a food type in a scat or GI tract, omitting bait, plant debris, and unidentifiable items. Percentages are yearly weighted averages of 5 seasons, where the weighting factor is the number of days in each season. Percentages do not total 100% because foods outside of the 7 major groups are excluded.

Table 3. Food niche-breadth comparisons among 5 seasons, as measured by 3 indices: Brillouin's H (Brillouin 1960), Shannon's H' (Shannon and Weaver 1963), and Levins's B (Levins 1968), for fishers in Massachusetts and southwestern New Hampshire, 1992-1994. Indices are the averages of 25 subsamples (subsample $n = 14$ for each season) drawn from a larger sample of 211 scats and GI tracts for which season was known. Seasons are arranged in descending order of diversity in the fisher diet.

	H		H'		B	
	index	rank[a]	index	rank	index	rank
Deer-hunting	0.72	1[d]	0.91	1	7.34	1
Spring	0.66	2[c,d]	0.83	2	5.89	2
Winter	0.64	3[b,c]	0.82	3	5.38	3
Early Autumn	0.62	4[b]	0.67	4	4.04	4
Summer	0.40	5[a]	0.44	5	2.16	5
Overall	0.71		1.06		8.00	

[a] Values with the same superscript letter were not significantly different (nonparametric Tukey-type multiple comparison test, overall $\alpha = 0.05$ for the set of comparisons).

Seasonal Trends

Ranking seasons according to dietary niche breadth using the 3 indices produced similar results (Table 3). The nonparametric Tukey-type multiple comparisons test revealed that niche breadth (as measured by the Brillouin index) was significantly less in summer than in any other season, less during early autumn than during spring or deer-hunting season, and greater during deer-hunting season than every season except spring (overall $P < 0.05$).

Pronounced seasonal variation was also evident for the 7 main food types (Fig. 2). In winter, fruits, small murids, birds, and porcupines were uncommon in the diet, whereas eastern gray squirrels and raccoons were common. Raccoons and porcupines were absent from the diet in summer and early autumn, when fruits were common. Birds were absent from the diet in winter and early autumn.

Intraspecific Comparisons

No significant differences were detected between yearlings (age 1-2 years) and >2-year-olds ($P > 0.09$ for all 7 major prey, randomization test), so all fishers > 1 year of age were pooled and labelled "adults." The only significant difference between juveniles and adults was for raccoon; raccoons were eaten primarily by juveniles (Fig. 3; $P = 0.002$, randomization test). There was no significant difference in prevalence of raccoons in the diet between males and females

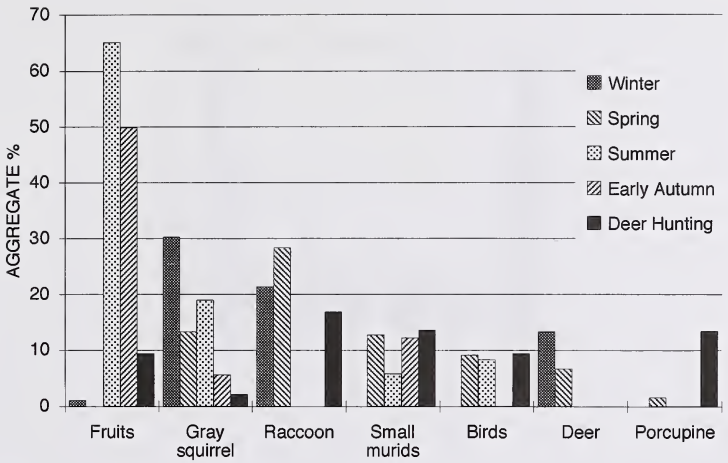

Figure 2. Variation among seasons in the diet of fishers in Massachusetts, 1992-1994. Seasons: winter (January to March, $n = 22$ scats), spring (April to May, $n = 52$ scats), summer (June to August, $n = 30$ scats), early autumn (September to October, $n = 48$ scats), and deer-hunting season (November to December, $n = 59$, 2 scats and 57 GI tracts). Data are average aggregate percentages of estimated volume of a food type in a scat or GI tract, omitting bait, plant debris, and unidentifiable items. Percentages do not total 100% because foods outside these 7 major groups are excluded.

(Fig. 4; $P = 0.211$, randomization test). Eastern gray squirrels were taken in significantly greater quantity by females than by males (Fig. 4; $P = 0.006$, randomization test).

Raccoon/Rabies Relationship

In towns where rabies was first reported in the same year that a given food sample was collected, the relative frequency (percentage of the total number of food occurrences in all food samples) of raccoons in the fisher diet was more than 3 times higher than in towns where rabies had not yet been reported; however, this result was not significant ($P = 0.049$, randomization test, Bonferroni $\alpha = 0.05/3 = 0.017$). In towns where rabies had already been reported the previous year, raccoon frequency was similar to levels in towns where rabies had not yet been reported.

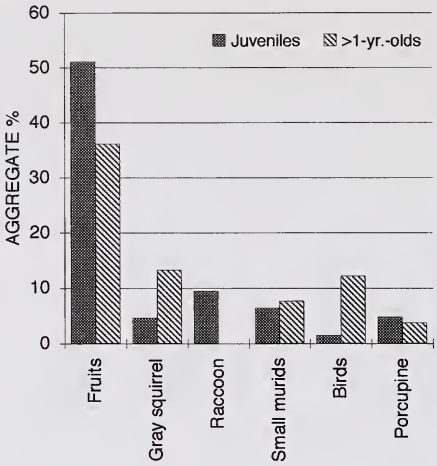

Figure 3. Age-related differences in use of major food groups by fishers in Massachusetts, 1992-1994 (juveniles: age 4-12 months; adults: age >1 year). Data are from scats (n = 154) and GI tracts (n = 57), and are average aggregate percentages of estimated volume of a food type in a scat or gastrointestinal tract, omitting bait, plant debris, and unidentifiable items. Percentages are yearly weighted averages of 5 seasons, where the weighting factor is the number of days in each season. Percentages do not total 100% because foods outside of the 6 major groups presented here are excluded.

Discussion

General Food Habits

The use of prey occurrence data in food-habits studies is problematic because some prey are more easily digested, or consist of a greater ratio of indigestible to digestible matter, than others. This problem creates a certain amount of bias in comparing different food items. We believe that the aggregate percent method reduces this bias compared with the percent occurrence method, but ideally, it would be desirable to be able to correct for the differential digestibility of various food types. In spite of this shortcoming (and in the absence of such correction factors for fishers), we believe this bias was fairly consistent in our study, and the niche-breadth indices we calculated should therefore be comparable. Furthermore, it should be possible to compare the prevalence of a specific food species (or even similar species such as lagomorphs, or small murids) between

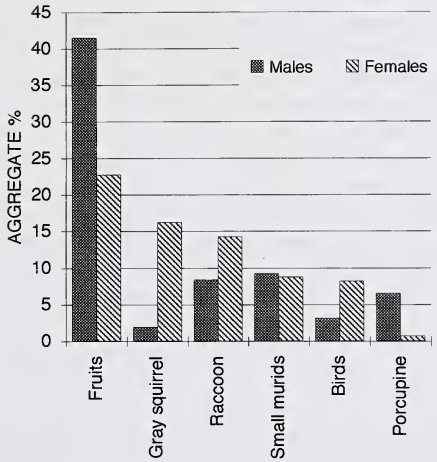

Figure 4. Sex-related differences in use of major food groups by fishers in Massachusetts, 1992-1994. Data are from scats (n = 154) and GI tracts (n = 57), and are average aggregate percentages of estimated volume of a food type in a scat or GI tract, omitting bait, plant debris, and unidentifiable items. Percentages are yearly weighted averages of 5 seasons, where the weighting factor is the number of days in each season. Percentages do not total 100% because foods outside of the 6 major groups presented here are excluded.

seasons, or among studies, although caution should be exercised when comparing the relative occurrence of different food items in the fisher's diet, particularly in the absence of food availability data.

Remains of eastern gray squirrels, the single most prevalent prey species in the diet of fishers in our study area, occurred more often than in other studies of fisher food habits (cf. Powell 1993). Most fisher resting sites were in squirrel nests (54%, n = 61; S. M. Powell, unpublished data), as was the case in Connecticut (Kilpatrick and Rego 1994). Thus, we suspect that fishers in our area may have climbed trees with visible leaf nests to search for resting squirrels. Kilpatrick and Rego (1994) found no significant difference between the proportion of tree nests used by males and females, even though in our study females ate significantly more squirrels than males did. This observation suggests that fishers also may select these nests simply because they are good resting sites.

Porcupine, often considered to be a staple food of fishers (Powell 1993), occurred relatively infrequently in our samples. This result is similar to those of

other studies in the northeastern US and Ontario (deVos 1951, Brown and Will 1979, Arthur et al. 1989, Giuliano et al. 1989). This low use may reflect the greater relative availability of alternative prey types (Giuliano et al. 1989), but this statement could not be tested because we did not measure prey availability.

Snowshoe hares, the most commonly occurring prey species in the diet of fishers in North America (Powell 1993), were uncommon food items in our study. Our percent occurrence for this species was similar to that found in New Hampshire by Kelly (1977). Fishers are known to respond to hare population cycles by changing their relative utilization of alternate food types (Leonard 1980, Raine 1981, Kuehn 1989, Powell 1993). The low incidence of snowshoe hares in the diet of fishers in our study area, however, probably results from the current successional stage of these forests, which may not be able to support large hare populations (T. A. Decker, MDFW, and W. Healy, United States Forest Service, pers. commun.; cf. Litvaitis et al. 1985, Litvaitis 1993).

Studies of mustelid food habits have generally indicated a highly carnivorous diet. However, the high prevalence of fruits in the diet of fishers (cf. Rego 1984, Arthur 1987) indicates that this species is not strictly carnivorous, and may actually specialize in non-animal food sources during certain times of the year (see below). When fruits are abundant, they require relatively little searching and handling time. The generalist nature of the fisher diet (as indicated by the large diversity of food types consumed) facilitates the exploitation of alternate foods as they change in relative abundance.

Seasonal Trends

The food base for terrestrial predators in northern latitudes can be extremely variable seasonally. For example, small rodents may be less available to fishers in winter due to snow cover or reduced abundance (Merritt and Merritt 1978, Hayward 1989), deer may be more available in winter due to persisting hunter-killed remains (Clem 1977) or to natural mortality, and fruits are not present for much of the year. The high seasonal variability we observed for all major fisher food groups in our study area indicates that fishers are not the obligate specialists of the northern coniferous forest-snowshoe hare-porcupine complex that they were once believed to be. Fishers presumably specialize in snowshoe hares and porcupines in other regions because they are common (or commonly accessible) there, or because alternate prey are scarce, or because they are energetically efficient prey for fishers in those habitats. Our data do not indicate whether certain foods are sufficiently limiting during certain seasons to force fishers to alter their diet. However, they do at least suggest that fishers have the capacity to take advantage of alternate foods as preferred (or commonly eaten) foods change in relative abundance either seasonally, episodically, or geographically.

One implication of this flexibility in the diet of fishers is the potential minimization of competition with other predators. There is no convincing evidence that fishers are strong competitors with other carnivores, even in areas where fishers feed heavily on a narrow range of species that may also be commonly used by other carnivores (e.g., snowshoe hares, which may be shared as prey with bobcats [*Lynx rufus*] and coyotes [*Canis latrans*]). However, if a common food resource becomes limited in availability or abundance, the ability of the fisher to shift its diet to alternative foods would reduce niche overlap, and therefore reduce the potential for competition. This flexibility may be important for fishers that are introduced into new areas, where potential competition for limited prey populations might otherwise limit the ability of fishers to become established.

It is possible that competition with other predators might be more severe in certain seasons. For example, reduced rodent availability in winter might lead to greater competition with foxes, weasels, owls, and other predators of rodents. However, the low incidence of small murids in the winter diet of our fishers neither supports nor refutes possible competition for this food type with other predators. Without carefully controlled experiments where resource abundance is artificially controlled, it is difficult to demonstrate competition in the field, especially with a wide-ranging species such as the fisher.

The few previous seasonal studies of fisher diets have revealed either no significant seasonal differences (Clem 1977), differences bordering on significance (Coulter 1966), or a difference in only 1 food type (e.g., birds; Coulter 1966). These results may be due to the narrow seasonal time spans over which diets were examined (Martin 1994). The strong seasonal differences we observed demonstrate the inappropriateness of making inferences of the overall diet of fishers based on a single season's data, or comparing dietary studies based on data from different seasons.

Intraspecific Comparisons

The reason for the greater prevalence of squirrels in the diet of female fishers is unclear, but female fishers may be more efficient predators of squirrel-sized prey or more arboreally agile than the larger males, whereas males may eat more fruits and porcupines. Although the differences between males and females for fruits and porcupines were not significant, the incidence of embedded porcupine quills was higher in males in this (E. C. York, unpub. data) and other studies (Coulter 1966, Kelly 1977, Rego 1984, Douglas and Strickland 1987, Arthur et al. 1989, Kuehn 1989). Previous studies failed to detect significant sex-related differences in diet (Coulter 1966, Clem 1977, Kelly 1977, Kuehn 1989).

Although our findings were not significant, Giuliano et al. (1989) also reported that juvenile fishers ate more fruits than adults did. This finding may be related

to the inexperience of juveniles at capturing prey (Raine 1979). The higher occurrence of the raccoon, a large and potentially dangerous prey in the diet of the relatively inexperienced juveniles, as compared with adults, is rather counterintuitive. However, it is possible that juveniles fed mainly on raccoons as carrion (see below), or that they fed mainly on young raccoons.

Raccoon/Rabies Relationship

The suggested higher incidence of raccoons in the diet of fishers in areas where rabies had recently occurred advances the possibility of a causal relationship. During the early stages of the epidemic, the death of large numbers of infected raccoons may have led to an abundance of raccoon carrion for fishers. T. A. Decker (MDFW, pers. commun.) commented that many of the raccoons in any given locality in Massachusetts may have succumbed to the disease within 3-4 weeks of the time when rabies first entered the area. Alternatively, rabies-symptomatic raccoons may be more easily found and killed by fishers. If fishers encounter raccoons while they are still alive, then there is a substantial risk of fishers being exposed to the virus (to date 1 fisher has been reported with rabies in Massachusetts by the MDFW). Because juvenile fishers ate more raccoons, juveniles may be at greater risk of exposure to rabies than adults. The increased utilization of raccoons by fishers appeared to be temporary. After the initial presumed abundance of dead or ill raccoons, fishers probably encountered them less frequently and shifted their diet back to more commonly available food types.

Niche-Breadth Indices

Several niche-breadth indices have been proposed for food-habits studies. The Shannon index was presented here for comparison with Martin's (1994) niche-breadth calculations for fishers, but Levins's (1968) B may be more appropriate in some circumstances (Hurlbert 1978, Hair 1980, Krebs 1989) and is presented because other carnivore studies have used this index for comparative purposes. However, the Brillouin index is the most appropriate measure if samples are non-random (Pielou 1966, 1967, 1975; Zar 1984; Brower et al. 1990). Because many food-habits studies (including ours) involve collecting scats from non-random sites such as maternal dens, tracking specific radio-tagged animals, or collecting GI tracts from animals that are most easily trapped, it is inappropriate to use indices that require random samples.

Martin (1994) calculated Shannon indices for 12 fisher studies in North America, and concluded that midwestern and western fisher populations had less diverse diets than eastern populations. However, none of these studies were year-round, and possible seasonal differences were not investigated. Our overall Shannon index (1.06) was comparable to Martin's (1994) summaries of other eastern studies, and was greater than the average of 0.92 (Martin 1994).

However, values varied greatly among seasons, and our H' of 0.44 for summer was lower than for any of the midwestern or western studies.

Diversity indices also can be affected by sample size (Kruuk 1986, Brower et al. 1990) because more food types tend to be identified as more samples are examined. Because sample sizes of the studies summarized by Martin (1994) varied widely (from 18 to 490), the indices are not comparable. However, Clevanger (1994) found no significant relationship between niche breadth and sample size for his comparisons using Levins's B. Because our objective was to compare seasonal differences for a single fisher population, and because we compared equal sample sizes from each season, we believe that our data are valid for our seasonal comparisons, but are not necessarily comparable to other fisher studies.

A final consideration is that niche-breadth indices decrease when the number of resource categories is reduced by lumping (Petraitis 1979). In our study, niche breadths were narrowest during the summer probably because the widespread availability of fruits allowed fishers to reduce their consumption of animal prey that are eaten during other seasons. However, if we were to treat each fruit species as a separate food type, our summer niche-breadth values would increase greatly, and our conclusions would be reversed.

Management Implications

The fisher has long been valued as a furbearer, but more recently as an intrinsic part of wild areas as well. In some regions their numbers fluctuate in synchrony with the 10-year snowshoe hare cycle (Bulmer 1974), but fisher populations are generally limited by the human harvest, not by food (York and Fuller 1994). Our food-habits data add to the notion that fishers are generalist predators that eat a variety of foods, and except under unusual circumstances where food is generally limited, populations can increase substantially if fisher trapping is limited (York 1996).

The historic range of fishers was substantially reduced during the late 19th and early 20th centuries (Powell 1993), and numerous reintroductions into their former range have occurred recently (Berg 1982, Proulx et al. 1994). Although "habitat" considerations (i.e., food) have been acknowledged as important (Berg 1982), it seems more likely that other factors, such as other predators, human harvesting, and time of release are more important to successful reintroductions.

Further investigation of fisher diet may be important in areas where a fisher harvest is to continue, and where potential food availability is thought to fluctuate greatly. Investigators undertaking such food-habits studies should attempt to collect samples throughout the year because of the potentially serious biases of attempting to make inferences to the overall diet of a predator based on data from

only part of the year. If logistical, temporal, or budgetary constraints prohibit complete data collection, then it must be recognized that data from only part of the year are not necessarily representative. Furthermore, caution should be exercised in comparing studies based on data from different seasons. Age- and sex-related differences also should be examined wherever possible, particularly in dietary studies that may be biased toward particular subpopulations (e.g., due to differences in trappability, or to non-randomly collected food samples).

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Part IV

Techniques

Martes: taxonomy, ecology, techniques, and management, pages 309-316.
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USE OF IMPLANTABLE MICROCHIPS FOR INDIVIDUAL IDENTIFICATION OF FISHERS

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Abstract: We tested the applicability of passive-integrated transponder (PIT) tags for marking individual fishers (*Martes pennanti*). We implanted PIT tags in 40 young kits (6-12 weeks old), 5 juveniles (4-12 months old), and 15 adult (>1 year old) fishers. Some of the kits (n = 10) were also marked with plastic eartags, and all adults and juveniles were marked with plastic or aluminum eartags and a radio-collar. For comparison, 9 kits were marked with plastic eartags only and 73 juveniles/adults were marked with plastic or aluminum eartags and radio-collars only. Eighteen PIT-tagged fishers (8 kits, 10 juveniles/adults) were recaptured 5-8 months after implantation and all retained the PIT tag. However, 2 of 7 kits and 4 of 53 juveniles/adults recaptured an average of 11 months (range = 3-27 months) after initial tagging had lost both eartags, and 12 of 92 juvenile/adult fishers had shed their radio-collar. PIT tags seem a reliable method of long-term individual identification of fishers. Advantages and disadvantages of this method relative to traditional methods are discussed.

Introduction

Studies of population dynamics and structure rely on individual identification of animals (Pollock et al. 1990). Techniques used to mark individuals must be identifiable, unobtrusive, unambiguous, and must remain intact for the duration of the study (Elbin and Burger 1994). Several methods have been used to individually mark wild and captive fishers (*Martes pennanti*), including applying plastic (this study) and metal (Arthur 1988) eartags, tattooing, or a combination of both (Douglas and Strickland 1987). Although plastic and metal eartags provide a readable external tag for many species, tag loss is common (Alt et al.

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1985, Hubert et al. 1985). Additionally, ear tagging of newborn and very young individuals is difficult because of their small size and lack of ear development, or their mothers may chew off the tags. Tattoos have been used successfully in conjunction with eartags for juvenile and adult fishers (Douglas and Strickland 1987), but unsuccessfully for other mustelids (Fagerstone and Johns 1987, Thomas et. al. 1987).

Implantable passive integrated transponder (PIT) tags have been used to individually mark wild black-footed ferrets (*Mustela nigripes*, Fagerstone and Johns 1987), sea otters (*Enhydra lutris*, Thomas et al. 1987), black-tailed prairie dogs (*Cynomys ludovicianus*, Fagerstone and Johns 1987), bats (e.g., *Eptesicus fuscus*; Barnard 1989), white storks (*Ciconia ciconia*, Michard et al. 1995), salmonids (Hamner 1989), various reptiles and amphibians (Camper and Dixon 1988, Germano and Williams 1993, Elbin and Burger 1994, Freeland and Fry 1995), as well as many other captive (Elbin and Burger 1994) and domestic species. Few failures (6% of 673 cases) of PIT tags have been reported (Fagerstone and Johns 1987, Thomas et al. 1987, Camper and Dixon 1988, Barnard 1989, Hamner 1989, Ball et al. 1991, Germano and Williams 1993, Elbin and Burger 1994). We evaluated the effectiveness and applicability of PIT tags as permanent markers for fishers and compared fisher PIT tag retention rates to eartag and radio-collar retention rates.

Methods

Fishers were initially captured and tagged in a 210-km^2 study area in north-central Massachusetts, and recaptured in the study area or in adjacent southern New Hampshire. Adult (>1 year old) and juvenile (4-12 months old) fishers were captured in cage-type traps and immobilized with intramuscular injections of ketamine hydrochloride (Ketaset, Aveco Co. Inc., Fort Dodge, Iowa), at dosages of 12-33 mg/kg body weight (Arthur 1988). Uncollared juvenile fishers resting with their radio-collared mothers and previously radio-collared adults were captured using darts delivered from a Vario Air Rifle (Telinject USA, Inc., Saugus, California). Fisher kits (6-12 weeks old) were hand-captured at maternal dens (Paragi 1990). Larger kits (8-12 weeks old) were immobilized with ketamine (12-33 mg/kg); other kits were handled and tagged without immobilization.

Fishers were sexed and weighed, and body measurements were recorded. A first upper premolar was extracted from adults and juveniles and sent to Matson's Laboratory (Milltown, Montana) for estimating age from counts of cementum annuli (Arthur et al. 1992, Poole et al. 1994).

Adult and juvenile fishers were marked with a self-piercing, numbered, plastic rotary type (Minitags, Dalton Supplies Ltd, Oxon, England) or aluminum (Monel No. 1, National Band and Tag Co., Newport, Kentucky) eartag in each

ear and fitted with radio-collars (Model 080 or 205, Telonics Inc., Mesa, Arizona; or Model 16M, ATS Inc., Isanti, Minnesota). Additionally, some animals were marked with implanted 2.1 × 11.0 mm PIT tags (125 kHz, model TX1400L, Destron/IDI, Boulder, Colorado). The transponder tag consisted of a microchip and electromagnetic coil, sealed in biocompatible glass. Kits were marked with Minitags, PIT tags, or both and returned to the den. Smaller (6-8 weeks old) fisher kits' ears were too small for Minitags so they were tagged with PIT tags only; larger kits were tagged with both tags.

Minitags were affixed in the approximate center of the ear, and Monel tags were attached at the base of the anterior edge of the ear. The PIT tags were injected with a 3-cc syringe modified with a plunger and 12-gauge hypodermic needle. The PIT tags were placed subcutaneously at the base of the skull, posterior to the sagittal crest, and medial to the ear. The tag emitted a 10-digit alphanumeric code (programmed when manufactured) when activated by an electromagnetic signal from a battery-operated, portable hand-held reader (Handi Reader, Destron/IDI, Boulder, Colorado). All tags were read immediately after implantation to ensure that the chip was working. To minimize the potential of infection, eartags and PIT tags were rinsed with isopropyl alcohol before being affixed (Paragi 1990, Elbin and Burger 1994).

From October 1992 to June 1995, 130 fishers were marked with eartags, PIT tags, radio-collars or a combination of two or more tag types. Forty-nine (27 M, 22 F) fisher kits were captured and marked. Of these, 30 (16 M, 14 F) were marked with PIT tags only, 9 (6 M, 3 F) were marked with eartags only, and 10 (5 M, 5 F) were marked with two eartags and PIT tags. All juveniles and adults were tagged with Minitags (29 M, 43 F) or Monel eartags (3 M, 5 F) and fitted with a radio-collar. In addition to eartags and collars, PIT tags were implanted in 4 (2 M, 2 F) juveniles and 15 (8 M, 7 F) adults. Eleven (4 M, 7 F) fishers that were marked as kits were also captured as juveniles and radio-collared and eartagged if eartags had not been attached previously (1 M, 4 F). One female (eartagged as a kit) that was not PIT-tagged as a kit was later PIT-tagged as a juvenile.

Live-recaptured, marked fishers and carcasses of dead marked fishers were inspected for eartags and radio-collars, and the animals were scanned extensively around the head, neck and shoulders with the PIT-tag reader for the presence of a PIT tag. Marker presence or absence was noted and lost tags were replaced in live-captured animals. Harvested fishers marked with PIT tags were skinned and the carcass and pelt was inspected visually for the tag. Two captive fishers were marked with PIT tags as kits and tags were read weekly. Captive fishers were radiographed 12 weeks post-tagging to examine PIT tags.

We determined relative retention of eartags (Minitags only) by examining all recaptured marked fishers with radio-collars or PIT tags for the presence or absence of 1 or both eartags. Retention of PIT tags was determined by examining

all recaptured fishers with eartags or radio-collars (that were initially marked with PIT tags as well) for the presence or absence of PIT tags. We used SURVIV (White 1983) to estimate tag-loss rates for juveniles/adults and for combined kit and juvenile/adult tag-loss rates. Recaptures of fishers initially captured as kits were combined into 2 4-month intervals, and fishers tagged as juveniles or adults were combined into 6 4-month intervals. Because recapture sample sizes were small, we used a constant parameter model in which retention rates were considered to be equal for all capture periods for kits and adult/juveniles (J. Hestbeck, pers. commun.). Four-month radio-collar loss rates were calculated using MICROMORT (Heisey and Fuller 1985) by substituting a slipped radio-collar for a mortality.

Results

Eight (2 M, 6 F) fishers PIT-tagged as kits and 10 (2 M, 8 F) tagged as juveniles/adults were recaptured 1-17 ($\bar{x} = 7$) months after implantation, and all had retained the PIT tag (Table 1). Captive fishers' PIT tags were read weekly for 13 weeks post-tagging, resulting in 13 successful readings for each fisher. All PIT tags remained readable within 1-2 cm of the implantation site. However, the PIT tag of 1 of the captive kits migrated approximately 5 cm from the implantation site (as seen from radiographs). Six adult female fishers with PIT tags were harvested 6-13 ($\bar{x} = 10$) months post-tagging. After skinning, tags were found in the subcutaneous tissue between the pelt and the remainder of the carcass.

Of 8 (4 M, 4 F) kits recaptured 2-5 ($\bar{x} = 4$) months after tagging, 4 (3 M, 1 F) had lost at least 1 eartag (retention rate = 0.47, SE = 0.18), and 2 (1 M, 1 F) of these kits had lost both eartags (retention rate = 0.75, SE = 0.20). Of 53 (14 M, 39 F) eartagged juveniles/adults recaptured 1-27 ($\bar{x} = 11$) months after initial tagging, 17 (5 M, 12 F) had lost at least 1 eartag (retention rate = 0.84, SE = 0.04), 2 of these (1 M, 1 F) had lost both eartags (retention rate = 0.98, SE = 0.02) (Table 1).

Eartag retention rates for kits and juveniles/adults did not differ ($Z = 0.78$, $P = 0.29$; $Z = 0.49$, $P = 0.35$; at least 1 and both eartags, respectively). Eartag retention rates for all ages combined were 0.97 (SE = 0.02) and 0.82 (SE = 0.04) for at least 1 and both eartags, respectively.

Only 1 recaptured male adult had shed his radio-collar; however, 11 others (4 M, 7 F) had shed collars but were not recaptured. Most radio-collars were slipped within 3 months after tagging ($\bar{x} = 82$, range = 6-236 days). Four-month radio-collar retention rates did not differ for males (0.94, SE = 0.02, $n = 10{,}083$ radio-days) and females (0.95, SE = 0.02, $n = 16{,}763$ radio-days; $Z = 0.26$, $P = 0.39$). Pooled collar retention rate for males and females was 0.95 (SE = 0.01, Table 1).

Table 1. Tag retention rates of passive integrated transponder (PIT) tags, Minitags (plastic eartags), and radio-collars in kit and juvenile/adult fishers.

	No. captured		$\bar{x}$ months captured post-tagging		Retention rate (SE)	
Marker type	Kits[a]	Juv./adults[b]	Kits[a]	Juv./adults[b]	Kits[a]	Juv./adults[b]
PIT tags	8	10	6	7	1.0	1.0
Minitags	8	53	4	11	0.75 (0.20)[c]	0.98 (0.02)[d]
Radio-collars	—	92	—	10	—	0.95 (0.02)[e]

[a] Fishers tagged as kits (6-12 weeks old).
[b] Fishers tagged as juveniles (4-12 months old) or adults (>1 year old).
[c] 4-month retention rate of at least 1 eartag, from age 6-12 weeks to age 4-12 months estimated using SURVIV (White 1983)
[d] 4-month retention rate of at least 1 eartag, from age >4 months estimated using SURVIV (White 1983).
[e] 4-month retention rate calculated from 26,846 radio-days using MICROMORT (Heisey and Fuller 1985).

Discussion

The PIT tags seem a reliable method of long-term individual identification of fishers. We found PIT tags especially useful in marking fisher kits that were too small to effectively mark with eartags. Some kits lost their eartags within a few days of tagging, probably from being chewed off by their mothers; others lost tags throughout the summer. Because there is no internal power source, PIT-tag life is theoretically indefinite, so tags implanted into kits should remain functional throughout the entire life of the animal. The PIT tags implanted into adult fishers provide a backup marker if eartags or the radio-collar are lost.

We found that PIT tags were quickly and easily implanted in fishers of all ages. Even young fishers (6-8 weeks old) that were not immobilized showed little physical reaction to the implantation of the tags. Implantation sites showed no signs of infection or damage from the tags, and we found that all PIT tags remained readable from the implantation site. Though a tag in one of the captive fishers had migrated, the distance was short (5 cm) enough that the tag was readable from the implantation site.

Despite the effectiveness and potential long life of the PIT tag, there are several disadvantages compared to traditional tagging methods. Initially, the cost of the reader ($400 US for a portable reader) or the tags ($4-8 US each, depending on the quantity) is substantially higher than that of eartags and tattooing. Second, the lack of a visible tag makes it impossible for the researcher to identify the animal, and without a reader, carcasses and fresh pelts from harvested animals must be inspected carefully to visually locate the tag. Finally, although animals marked with PIT tags do not need to be immobilized to accurately read the marker, the system is limited by the short distance required to activate the chip and the animal must be held in a device that does not produce environmental interference to the reader (Freeland and Fry 1995). Long (>5 cm) migrations of the tag (Burk 1995) would require extensive scanning of the animal to accurately determine the presence or absence of the tag.

Despite the disadvantages of this system, we feel that PIT tags are a useful marker for permanent identification of fishers and other *Martes* species, especially in marking very young individuals. We believe that PIT tags will remain operative throughout the life of animal and would be beneficial for long monitoring periods when traditional markers could be lost.

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CAPTIVE CARE AND CLINICAL EVALUATION OF FISHERS DURING THE FIRST YEAR OF A REINTRODUCTION PROJECT

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Abstract: In 1994, in cooperation with the Pennsylvania Game Commission, we developed and implemented the Pennsylvania Fisher Reintroduction Project to restore extirpated fishers (*Martes pennanti*). During the first year of the project, 45 fishers were live-trapped in New Hampshire and New York and transported to The Pennsylvania State University (PSU) for prerelease care and clinical evaluation. While at PSU, fishers were caged individually in climate controlled animal rooms for a mean period of 18.7 days (6 to 41 days) to facilitate the following: (1) quarantine as a precaution against translocating infectious disease; (2) treatment of capture-related injuries; (3) conditioning on a high caloric diet; (4) collection of blood samples to establish a clinically normal

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range of hematology and blood chemistry values; (5) comparison of responses to various chemical restraints (tiletamine hydrochloride [HCl]/zolazepam HCl, ketamine HCl/xylazine HCl, and ketamine HCl); and (6) evaluation of immune response to canine distemper vaccine. We reviewed results of these initial evaluations and the associated implications for enhancing captive care and management protocols during subsequent years of the fisher reintroduction project.

Introduction

Historically, fishers (*Martes pennanti*) were widely distributed in Pennsylvania (Hagmeier 1956, Cunningham 1985) but became extirpated, presumably because of unregulated trapping and extensive timber harvesting during the 1800's and early 1900's (Cunningham 1985). Fishers are now classified as endangered/extirpated in the state (Kirkland and Krim 1990).

In cooperation with the Pennsylvania Game Commission (PGC), we determined, based on review of current conditions and success of other fisher reintroduction projects (Pack and Cromer 1981, Berg 1982), that fishers potentially could be reestablished in Pennsylvania (Serfass et al. 1994). To facilitate restoration of fisher populations, the Pennsylvania Fisher Reintroduction Project (PFRP) was developed and implemented in 1994.

Prior to release, fishers underwent a captive care and monitoring program designed to enhance their health and condition and to reduce the risk of releasing animals infected with contagious disease. Protocols for the captive management program were modeled after those developed during a similar project that restored extirpated river otter (*Lontra canadensis*) populations to portions of Pennsylvania (Serfass et al. 1993) and other projects that successfully managed fishers in captivity for reintroduction programs, research, or zoo displays (LaBarge 1987, Cole and Proulx 1991, Frost and Krohn 1994, Proulx et al. 1994). Our overall objectives were to develop and evaluate protocols for trapping and transport, veterinary care and clinical evaluation, and housing, diet, and other captive requirements of fishers. Specific objectives associated with veterinary and clinical aspects of the captive management program included the following: (1) develop a database of hematological and blood chemistry values for clinically normal fishers; (2) evaluate response of fishers to various chemical immobilants; and (3) determine incidence of fishers with pre-existing titers to canine distemper and evaluate their immune response when vaccinated against canine distemper.

Methods

Procurement and Transport of Fishers

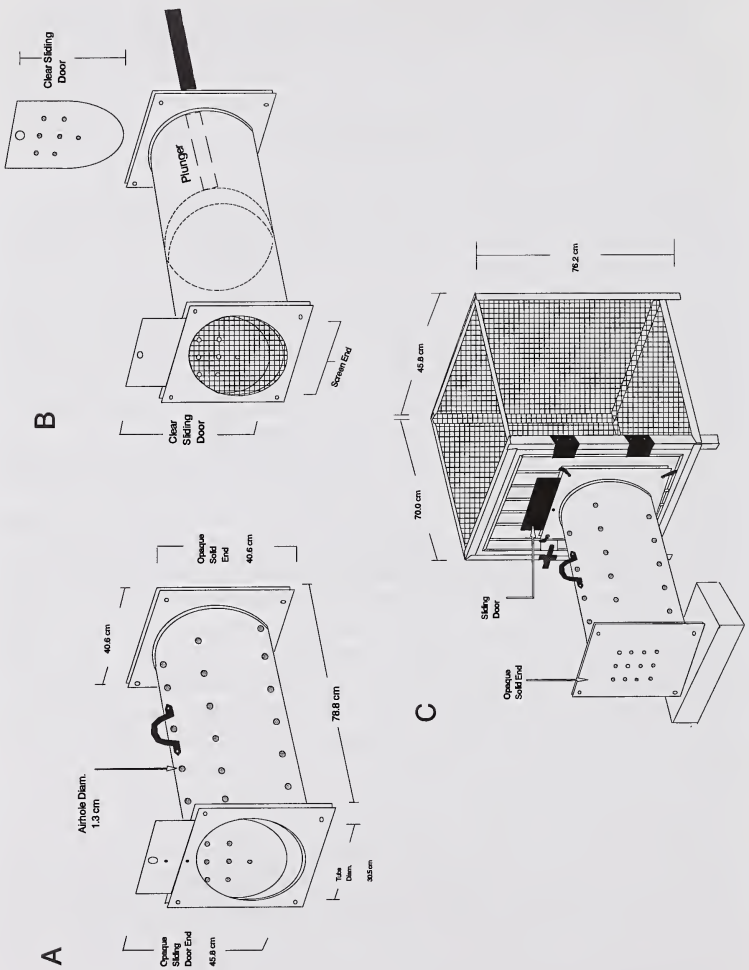
Fishers reintroduced in Pennsylvania were captured in wooden box-traps and cage traps by trappers in New Hampshire and New York during fisher trapping seasons (Nov. and Dec. 1994). Trappers were paid $100 for male and $150 for female fishers. Trapping protocols and logistics associated with obtaining fishers from trappers and transporting them to Pennsylvania were coordinated through personnel with the New Hampshire Fish and Game Department and the New York Department of Environmental Conservation.

Fishers were transferred from traps to individual, well-ventilated transport tubes (modified from Serfass et al. 1993) constructed from 0.6-m or 0.8-m sections of 30-cm diameter polyvinyl chloride (PVC) tubing (Fig. 1). Interchangeable PVC sheets (40.6 × 40.6 × 0.64 cm) connected to tube ends served as attachments for doors and components that facilitated restraint of fishers for administering immobilizing drugs (Fig. 1). All materials used to construct the tube were nonporous and easily sanitized with a disinfectant (1-Stroke Environ, Sanofi Animal Health, Inc., Overland Parks, Kansas 66210), and met requirements set forth by the Institutional Animal Care and Use Committee at PSU.

Fishers were transported to PSU by commercial airline while confined individually in transport tubes. Although we preferred to obtain fishers soon after capture, logistics associated with transfer of fishers among trappers, cooperating biologists, and airports often prohibited immediate transport. Because of convenience, cost-effectiveness, and time constraints, at least 3 to 6 fishers usually were obtained before arranging air transport. In these cases, fishers were held separately in 100 × 50 × 50-cm cages constructed from 2.54 × 2.54-cm welded steel wire, fed combinations of venison, beaver (*Castor canadensis*), and ground beef and provided drinking water *ad libitum*. Prior to transport, cloth towels or cedar shavings were inserted in tubes to cushion the fisher during airline transport and water was provided through a sipper tube inserted through a ventilation hole.

Housing

At PSU, fishers were housed individually in stainless steel cages (70 × 46 × 76 cm or 102 × 76 × 76 cm) placed in 3.6 × 3.4-m climate-controlled animal rooms designed for disease containment. Cage floors were 2.54 × 2.54-cm stainless steel mesh, which allowed feces, urine, and food materials to pass into a collecting tray. Cages were cleaned with water and liquid detergent every 2 days and disinfected weekly. No other species were housed at the facility during the project. Transport tubes were attached to cages to serve as a den box (Fig. 1). Eight or fewer fishers were housed in a single animal room and visual barriers were


A
Opaque Sliding Door End
45.8 cm
Airhole Diam. 1.3 cm
40.6 cm
Opaque Solid End
40.6 cm
78.8 cm
Tube Diam. 30.5cm
B
Clear Sliding Door
Plunger
Screen End
Clear Sliding Door
C
78.2 cm
45.8 cm
70.0 cm
Sliding Door
Opaque Solid End

maintained between fishers in adjacent cages. To minimize external stimuli and thereby reduce stress, lights in rooms housing newly arriving fishers were turned off for the first 48 hr. Photoperiod was subsequently adjusted to match ambient conditions. Room temperatures were maintained at 7° to 12°C and relative humidity between 40% and 70%.

Diet

We fed fishers a mixture of lean ground beef, commercial ferret chow (Lab Diet High Density Ferret Diet, PMI Feeds Inc., St. Louis, Missouri 63144), and a high caloric dietary supplement (Nutri-Cal®, Evsco Pharmaceuticals, Buena, New Jersey 08310) mixed at an approximate ratio by weight of 65:10:1, respectively. Food was provided once daily (LaBarge 1987, Cole and Proulx 1991). If the diet mixture was not accepted after 3 days in captivity, dead laboratory mice or strips of venison were added to encourage eating. Initially, the diet mixture was presented in quantities of 250 g for females and 400 g for males. After a fisher accepted the captive diet, the amount of food provided was adjusted until achieving maximal daily consumption (portion of food consistently remained uneaten after 24 hrs) with minimal waste. Water was provided *ad libitum*.

Health Evaluation

Each fisher underwent a complete health examination administered by a veterinarian within 1 to 3 days after its arrival at PSU. To facilitate initial examinations and subsequent reexaminations, fishers were immobilized with an injection containing approximately 30 mg (females) or 40 mg (males) tiletamine HCl/zolazepam HCl (TEL; Telazol®, Fort Dodge Laboratories, Inc., Fort Dodge, Iowa 50501) delivered at 50 mg/ml, a combination of 75 mg and 7.5 mg (females) or 110 mg and 11.0 mg (males) ketamine HCl and xylazine HCl (KET/XYL; Ketaset®, Fort Dodge Laboratories, Inc., Fort Dodge, Iowa 50501 and Rompun®, Miles Inc., Shawnee Mission, Kansas 66201) delivered at 100 mg/ml and 20 mg/ml, respectively, or 80 mg (females) or 145 mg (males) of ketamine HCl delivered at 100 mg/ml (Belant 1991, Cole and Proulx 1991, Roy 1991, Petrini

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Figure 1. Transport tube, interchangeable end components, and holding cage for fishers. Sliding doors or solid ends (A) were used during transport of fishers. To facilitate injection of immobilizing drugs, fishers were pinned against a screen end with a plunger inserted from the opposite end of the tube (B). Clear acrylic sliding doors were inserted to confine fishers to the tube and monitor condition and response to immobilants (B). Fishers were housed in climate-controlled animal holding rooms while confined individually in stainless steel cages (C). Transport tubes were attached to cages to serve as a resting area for fishers.

1992, Frost and Krohn 1994). Drugs were administered intramuscularly while fishers were restrained in the transport tube (Fig. 1). Heart and respiratory rates and rectal temperatures were monitored during immobilization. After losing the righting reflex, fishers were removed from the transport tube, weighed, ear-tagged (Monel Small Animal Ear Tag No.1005-4; National Band and Tag Co., 721 York Street, P.O. Box 430, Newport, Kentucky 41072), and examined.

Examinations focused on determining if trap-related injuries were sustained and detecting signs of clinical illness. Physical evaluation of muscle mass, fat reserves, and pelage condition were used as a preliminary index of overall health. Fishers were examined for ectoparasites by parting the fur throughout cephalic and cervical regions, the ventral abdomen, and base of the tail. Sex, and an estimation of age by examining development of the sagittal crest and tooth wear (Eadie and Hamilton 1958, Wright and Coulter 1967), were recorded during examinations. Abdomens of females were palpated to detect pregnancy. Underbelly markings of all fishers were photographed or illustrated to aid in post-release identification in the event that ear-tags were not retained.

We collected blood samples from the external jugular vein to establish a range of clinically normal blood values and to determine if fishers had been exposed to canine distemper. Blood samples were collected in anticoagulant blood collection tubes containing ethylene diaminetetraacetic acid (EDTA) and serum clot tubes and sent to veterinary diagnostic laboratories for analysis. Fishers were vaccinated for canine distemper (Fervac^{R}-D, United Vaccines, Madison, Wisconsin 53713) and given a subcutaneous injection of ivermectin (Ivomec^{R}, MSD-Agvet, Rahway, New Jersey 07065) at 200 µg/kg as a broad-spectrum parasiticide.

We immobilized fishers again 2 to 3 days prior to a scheduled release date to facilitate another physical examination, determine if injuries occurred during captivity, and attach radio-collars (19 fishers). Post-vaccination blood samples were collected to determine if the initial vaccination had stimulated an immune response to canine distemper virus. A second vaccination was administered if fishers remained in captivity ≥12 days following the initial vaccination. The decision to release a fisher was based on assessment of its health and condition (e.g., weight gain and no evidence of clinical illness) at the time of the follow-up examination.

Results and Discussion

Procurement and Transport

During the first year of PFRP, we handled 39 fishers from New Hampshire (18 males, 21 females) and 6 from New York (1 male, 5 females). Among these fishers, 44 were released in northcentral Pennsylvania. Most fishers (n = 26) were transported to Pennsylvania ≤2 days after capture, but 7 were held captive >50

days before transport ($\bar{x}$ = 9.8 days; range = 0-63 days). Trap-related injuries were low among the fishers handled by PFRP. A male received with damaged teeth (loss of 11 incisors; 4 canines, 3 upper premolars, and 6 upper molars broken to the gumline) was the only fisher to sustain injuries severe enough to preclude release. That fisher was sent to a zoo. A fisher from New Hampshire that died of undetermined causes before being transported to Pennsylvania was the only animal to die.

Fishers adjusted well to confinement in transport tubes. We detected no evidence of fishers injuring themselves during transport. Design of transport tubes reduced opportunities for fishers to injure teeth or paws by biting or scratching the container. Cloth towels and cedar shavings inserted in tubes appeared effective in cushioning and reducing stress. Airline cargo supervisors were satisfied with design of transport tubes and confident that fishers could not escape during transport.

Housing

Although captive behavior varied among individuals, all fishers appeared to adjust to captivity. Holding periods at PSU ranged from 6 to 41 days ($\bar{x}$ = 18.7; SD = 12.1). Duration of captivity was influenced by weather conditions at reintroduction sites and the health and condition of individual fishers. Fishers were acclimated to late fall and early winter conditions in New York and New Hampshire and appeared comfortable with room temperatures ranging from 7° to 12°C. We detected no evidence of aggressive or persistent escape behavior. Consequently, fishers did not injure teeth or paws by attempting to escape. Fishers became accustomed to using transport tubes attached to cages for refuge and resting. Sliding doors at the openings of transport tubes allowed animal caretakers to easily confine fishers so they could clean cages and provide fresh food and water.

Diet

All fishers accepted the captive diet. Periods until fishers began eating ranged from 1 to 4 days ($\bar{x}$ = 1.8 ± 0.94). Providing venison and mice with the captive diet was effective in stimulating fishers to begin eating. All fishers maintained or increased body weight while in captivity. Mean arrival weights were 2.56 ± 0.25 kg for females and 4.43 ± 0.61 kg for males. Among females, 24 (92%) gained weight ($\bar{x}$ = 0.32 ± 0.27 kg; range = 0.11-0.91 kg). Similarly, 18 (95%) males increased their body weights ($\bar{x}$ = 0.86 ± 0.77 kg; range = 0.23-2.9 kg).

Health Evaluation

Immobilants used during this project were all effective and relatively safe for immobilizing fishers for health evaluations. However, manual respiration through

endotrachial intubation and an intervenous injection of doxapram hydrochloride (Dopram®, AH Robins Co., 1407 Cummings Drive, Richmond, Virginia 23220) administered at 5 mg/kg were required to resuscitate 2 adult fishers (female and male) that underwent respiratory arrest after being immobilized with doses of approximately 29 mg/kg KET/2.9 mg/kg XYL and 21 mg/kg KET/2.1 mg/kg XYL, respectively. Induction times for these fishers were rapid (approximately 0.16 and 0.83 min, respectively). Physical examination and clinical chemistry results on these animals were within normal limits. No other cases of adverse responses to immobilants were detected.

Mean amounts (mg) of drugs administered to achieve immobilization varied (females - TEL: $\bar{x} = 31.9 \pm 5.7$, $n = 26$; KET/XYL: $\bar{x} = 75.5 \pm 20.4$ [KET] and 7.6 ± 2.0 [XYL], $n = 20$; KET: $\bar{x} = 83.0 \pm 17.9$, $n = 5$. males - TEL: $\bar{x} = 38.6 \pm 15.5$, $n = 22$; KET/XYL: $\bar{x} = 112.8 \pm 20.4$ [KET] and 11.3 ± 2.0 [XYL], $n = 18$; KET: $\bar{x} = 145.7 \pm 44.3$, $n = 7$). Large variation in restraint time was observed among immobilants. Time (minutes) from drug injection to recovery for fishers monitored throughout the immobilization period also varied (KET: $\bar{x} = 94.6 \pm 49.6$, $n = 9$; KET/XYL: $\bar{x} = 123.6 \pm 47.5$, $n = 35$; TEL: $\bar{x} = 225.3 \pm 106.1$, $n = 41$). Ongoing studies to evaluate induction times, recovery times, and physiological responses to these immobilants will continue during the second year of the reintroduction project.

Most injuries to fishers were minor and seldom required extensive medical treatment. An adult male fisher sustained a trap-related injury that required amputation of a toe. Another adult male developed an infection from puncture wounds of undetermined cause on the jaw. Administration of an injection of long-acting antibiotics (Flo-Cillin®, Fort Dodge Laboratories, Inc., Fort Dodge, Iowa 50501), while we immobilized fishers to examine and clean injuries, was successful in preventing and treating infection in the respective cases. With exception of the male with severe dental injuries, none of the fishers sustained dental injuries considered severe enough to inhibit them from effectively foraging.

We detected no evidence of fishers being infected with contagious disease. Rabies is prevalent in areas of New Hampshire and New York where fishers were captured. Based on discussions with a viral disease expert (C. E. Rupprecht, Centers for Disease Control and Prevention, Atlanta), we consider a captive confinement period of 10 to 14 days a reasonable period to allow rabies or other infectious diseases to express clinical signs and thereby minimize risk of translocating the disease by releasing infected individuals (Serfass et al. 1995). Fishers in captivity are frequently vaccinated for rabies, canine distemper, and canine parvovirus (Cole and Proulx 1991, Petrini 1992). However, efficacy and safety of these vaccines have not been documented in fishers. None of the fishers examined had preexisting titers to canine distemper. Only 2 of 44 fishers developed a titer following a single vaccination against canine distemper (Fervac®-D).

Table 1. Summary of blood chemistry and hematology values for 44 clinically normal fishers (25 females, 19 males) examined during the first year of the Pennsylvania Fisher Reintroduction Project, 1994-95.

Measure	$\bar{x} \pm$ SD
Glucose (mg/dl)	150.98 ± 37.65
Blood Urea Nitrogen (BUN) (mg/dl)	20.86 ± 8.37
Creatine (mg/dl)	0.67 ± 0.13
BUN/Creatine (ratio)	33.01 ± 17.81
Cholesterol (mg/dl)	257.89 ± 50.02
Triglyceride (mg/dl)	64.84 ± 40.46
Sodium[a] (meq/l)	149.07 ± 5.71
PotassiumA (meq/l)	4.65 ± 0.33
Chloride[a] (meq/l)	109.33 ± 4.75
Bicarbonate[a] (meq/l)	21.45 ± 1.90
Serum Iron (µg/dl)	141.66 ± 38.40
Total Protein (g/dl)	6.48 ± 0.49
Albumin (g/dl)	3.41 ± 0.34
Globulin (g/dl)	3.05 ± 0.42
Albumin/Globulin (ratio)	1.15 ± 0.20
Alkaline Phosphatase (u/l)	56.86 ± 32.67
Serum Alanine Amino Transferase (u/l)	101.36 ± 110.15
Lactate Dehydrogenase (u/l)	364.09 ± 154.90
Aspartate Amino Transferase (u/l)	93.30 ± 48.22
Total Bilirubin (mg/dl)	0.17 ± 0.08
Calcium (mg/dl)	9.13 ± 0.50
Phosphorus (mg/dl)	4.75 ± 0.81
Hematocrit (%)	64.55 ± 5.05
Hemoglobin (g/dl)	15.60 ± 1.31
Red Blood Cell Count[a] (mil/mm^3)	6.95 ± 3.52
White Blood Cell Count[b] (thou/cm^3)	4.38 ± 2.30
Segmented Neutrophils[a] (%)	60.19 ± 15.02
Band Neutrophils[a] (%)	0.50 ± 0.89
Basophils[a] (%)	0.00
Lymphocytes[a] (%)	31.90 ± 11.19
Monocytes[a] (%)	2.76 ± 3.42
Eosinophils[a] (%)	4.55 ± 6.67
Mean Corpuscular Volume[a] (cu mic)	71.38 ± 4.11
Mean Corpuscular Hemoglobin[a] (pg)	17.21 ± 0.71
Mean Corpuscular Hemoglobin Concentration[a] (%)	4.19 ± 1.14

[a] $n = 42$
[b] $n = 41$

Among fishers failing to respond to the initial vaccination, 2 of 10 evaluated ≥14 days after administration of a second vaccination developed titers. Further evaluation of immune response to Fervac^{R}-D and another vaccine (Galaxy D^{R}, Solvay Animal Health, Inc., Mendota Heights, Minnesota 55120) will be conducted during year-2 of the project.

Knowledge of normal blood values improves diagnostic capabilities and thereby enhances opportunities for early intervention and treatment of clinical illness (Davis et al. 1992). Blood chemistry and hematology values have not been described for fishers. Consequently, clinically normal blood and hematology values (Table 1) established during initial phases of PFRP will be useful in assessing health of fishers obtained during subsequent years of the project.

Fecal flotations for parasitic ova and larva were evaluated before and after ivermectin administration when possible. Most fishers were infected with one or more species of ascarids, strongyles, and trichurids. Repeat fecal testing ≥3 days after administering 1 dose of ivermectin indicated efficacy against ascarids and strongyles, but little effect on the intestinal load of trichurids.

Conclusion

Implementing a predator reintroduction program requires a considerable commitment of time, labor, and financial support. Because of these constraints, usually only a limited number of animals can be reintroduced and opportunities to repeat reintroductions may not be available. Consequently, high survival among reintroduced individuals is necessary to assure a successful project. Release of healthy, well-conditioned animals will enhance the probability of a successful reintroduction program.

The PFRP has implemented a captive management program with the objective of enhancing the health and condition of fishers prior to reintroduction. Release of healthy, well-conditioned fishers was accomplished by developing transport techniques that reduced opportunities for injuries, promptly treating injuries, and encouraging weight gain by placing fishers on a high caloric diet in a controlled environment. Our ongoing investigations to establish a normal range of blood chemistry and hematology values, evaluate response to various chemical immobilants, and determine efficacy of vaccinating against canine distemper are designed to further enhance our ability to evaluate health condition of fishers and provide them medical care during future years of the reintroduction project.

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USING REMOTELY ACTIVATED CAMERAS TO MONITOR MATERNAL DENS OF MARTENS

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Abstract: Maternal dens are essential elements of American marten (*Martes americana*) habitat, yet information on how these structures are used is lacking. Since 1993, we monitored maternal dens by using remotely activated cameras. A burrow camera was sometimes used to verify the presence of kits prior to placement of external cameras. We used both 35-mm still cameras and 8-mm video cameras outside marten dens. Both types of cameras were activated by infrared sensors. We documented 1 or more martens in 1054 photographs or video events. Early in the denning period (May to early July), females were most often observed; kits began appearing the first 2 weeks of July. Adult males were observed at 6 of 16 dens. Specific behavioral traits included kit transfer; scent-marking; grooming; play; and prey capture, transfer, and consumption. The use of cameras proved effective for monitoring dens but they are somewhat problematic and have limitations. Video cameras provided more detailed information than 35-mm cameras.

Introduction

Use of cameras to visually record and describe biologically significant phenomena in field settings is not new (Gysel and Davis 1956, Dodge and Snyder 1960). Recently, however, use of cameras in wildlife studies has increased, and they have been employed in a variety of applications. A common use of still cameras is to detect the presence of wildlife (Joslin 1977, Mace et al. 1990,

Jones and Raphael 1993, Kucera and Barrett 1993, Raphael 1994). Still cameras have also been integrated into research for monitoring sites such as nesting structures (Picman 1987, Cowie and Hinsley 1988, Picman and Schriml 1994). Most studies using video cameras have been done in controlled settings. However, video cameras seem ideally suited to field studies because of the potential for continuous recording. For example, Houpt and Wollney (1989) described the time budgets and behavior of cattle over continuous 24-h periods by using video cameras. Closed-circuit television camera systems with remote lens and lighting (hereafter called burrow cameras) have been instrumental in some wildlife studies, particularly for verifying burrow or cavity occupancy (Speake and Altimere 1983, Spillers and Speake 1988).

Many researchers have referred to the importance of resting sites in studies of American marten (*Martes americana*) ecology (e.g., Buskirk 1984; Spencer 1987; Buskirk et al. 1989; Martin and Barrett 1991; Raphael and Jones, this volume), but maternal denning sites have received relatively little attention (Buskirk and Ruggiero 1994). Maternal sites are important to viability of the marten because they must provide protection from predators and the environment for the female parent (presumably under a maternally stressed condition) and her offspring. Most of the 13 studies documenting maternal dens (Buskirk and Ruggiero 1994) mention little more than the type of structure. In fact, the basis for most of the behavioral and developmental knowledge of martens comes from reports on captive animals (Ashbrook and Hanson 1927, Markley and Bassett 1942, Remington 1952). To date, only Hauptman (1979), Wynne and Sherburne (1984), Henry and Ruggiero (1993), and Henry et al. (this volume) provided substantial information on marten dens and the behavior and development of the inhabitants. Except for the study of Henry et al. (this volume), which used activity recorders, these studies depended on human observers, which could possibly bias results by altering the marten's behavior. Aubry et al. (this volume) also discuss the use of video cameras for fisher (*Martes pennanti*) den monitoring. In this paper, we discuss our use of cameras to help learn more about denning behavior without the need or bias of human observation. We emphasize the techniques used to monitor martens at maternal dens. We have included summaries to date and some anecdotal information that were recorded, but detailed analyses of marten behavior will not be reported until the study has been completed.

Study Area

The study area is located in south-central Oregon, about 15 km NE of Chemult. The topography is essentially flat, about 1675 m above sea level, but there are some nearby buttes, riparian depressions, and small ridges. There are several meadows present, usually along the riparian depressions. Most of the

area falls within the lodgepole pine (*Pinus contorta*)-bitterbrush (*Purshia tridentata*) community of the south-central Oregon pumice zone (Franklin and Dyrness 1973), but there are also stands or inclusions of ponderosa pine *(Pinus ponderosa*), true fir (*Abies* spp.), or mixed conifer.

Methods and Materials

Martens were captured in single-door wire live-traps (models 202 and 205, Tomahawk Live Trap Co., Tomahawk, Wisconsin) and immobilized with ketamine hydrochloride. We fitted animals with radio-collars (MOD-70, Config. 1A; Telonics, Mesa, Arizona) and located them from ground triangulation and walk-ins once or twice per week. Evidence indicates that parturition normally occurs from late April to early May in our area, so radio-tracking was intensified for adult females during this time to locate maternal dens. Several factors, including repeated site use, site exclusivity, reproductive history of the female, and visual or aural observations of kits, helped to determine which sites were maternal rather than resting (Raphael and Jones, this volume). We use the term maternal den (or den for short) to indicate a structure in which a female marten resides with her kits, or where the kits reside prior to independence (when kits no longer have close contact with the mother). This includes natal (where parturition occurs) and post-natal dens (= maternal dens, Henry and Ruggiero 1993). We lumped natal and post-natal dens for 3 reasons: (1) we could not claim with certainty that the first extensively used site was natal because we did not witness parturition; (2) we were not always certain that the first site we found with telemetry was indeed the first used; and (3) the term "maternal" implies care by the female parent, so the natal site should by definition be maternal. However, in keeping with Henry and Ruggiero (1993), we suspect the first extensively used sites that we found were indeed natal or immediately post-parturition sites.

The denning season of 1993 served as a pilot study. During that season, we evaluated the logistics of using 35-mm and video cameras by establishing camera stations at 3 dens. In most cases, the 1993 data reported in this paper refer only to the 35-mm cameras, because we only experimented with 1 video camera that year. The 1993 data allowed us to determine periods of activity outside dens. In 1994 and 1995 we recorded more detailed information on camera events and behavioral characteristics. From late April through May our emphasis was the location of martens at dens using telemetry. Cameras were usually established in June or July. We had only 2 video cameras and 8 35-mm cameras, so they were periodically moved between den sites. Camera use by den is outlined in Table 1.

During June to August 1995 we used a burrow camera (Burrow Probe III with Fieldcam MDP, Fuhrman Diversified, Seabrook, Texas) to help verify the presence of kits. The burrow camera consists of a video monitor and battery inside a

weatherproof housing, flexible cable, semi-flexible plastic sheath, and optical probe. The camera was used only when the female was absent from her den and the structure was accessible. The probe, fed into the nest chamber via the cavity entrance (Fig. 1), emits infrared light that can be picked up by the monitor, but the image is not in the visible spectrum. A video camera is connected to the monitor to record the image. The location of the female was periodically monitored with radio telemetry to warn us of her approach.

At 19 of 31 den sites (1 den was used in 2 different years), we mounted cameras to record events outside the entrance of the den (Table 1). Two types of camera system were used (Figs. 2, 3): 35-mm still cameras (Trailmaster, Goodson and Associates, Lenexa, Kansas) and 8-mm video cameras (Compu-Tech Systems, Bend, Oregon). Two models of camera bodies were used with the 35-mm systems, Olympus (AF-1 Twin, Olympus Corporation, Woodbury, New York) and Yashica (AW-Mini AF, Yashica, Inc., Sumerset, New Jersey). Both cameras were capable of recording date and time. The 35-mm system used 2 external sensors (Trailmaster model TM-1500), a transmitter and a receiver, to trigger the camera. The transmitter emits a wedge-shaped band of infrared light and the receiver picks up the light though a small lens, effectively reducing the wedge to a narrow beam (Kucera and Barrett 1993). An animal's interruption of

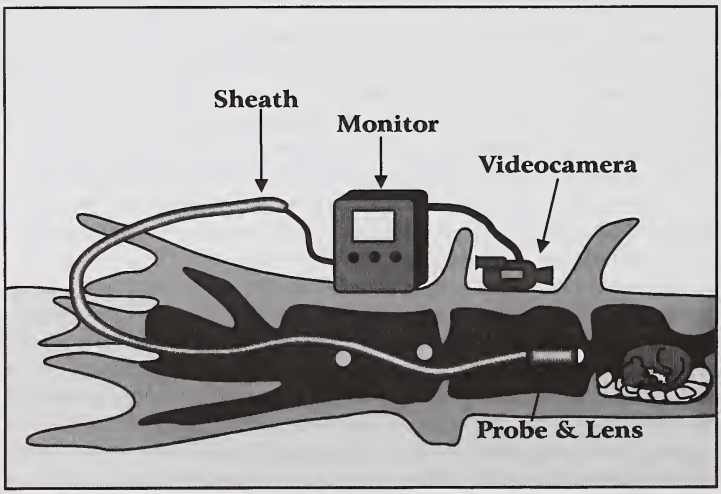

Figure 1. Longitudinal cross section of a log den showing a burrow camera system.

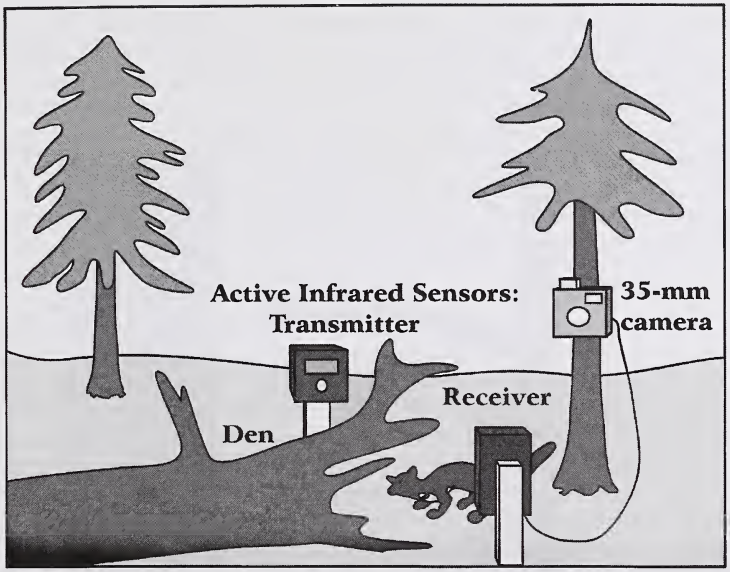

Figure 2. 35-mm camera system mounted at a log den.

the beam initiates an electronic signal that is transmitted from the receiver to trigger the camera. This active infrared system is activated only by motion. The receiving unit was programmed to the minimum delay setting of 6 seconds. The sensors were arranged so that a marten would need to pass through the beam to access or leave its den. Film in the camera is automatically advanced and rewound. The receiving sensor records every activation. Because of the design, this type of system was usually mounted near ground level, even if the den structure was a tree or snag. Because the camera lacks an effective telephoto lens and the sensors were at ground level, the camera was usually aimed near ground level also. Kucera and Barrett (1993) discussed this camera system in detail.

The video camera system is composed of an 8-mm video camera (Sony Electronics, Park Drive, New Jersey), a 12-volt motorcycle battery, an infrared receiving sensor, a timer, and a remote control device, all inside a protective housing. Peripheral support equipment includes a shotgun microphone, a fog lamp with red transparent cover (see Aubry et al., this volume), a deep-cycle marine battery, and a transmitting infrared sensor. The microphone and fog lamp were not used until 1995, so previous data were taken only with available light (>1 lux). The external sensor emits a wedge-shaped band of light and is triggered

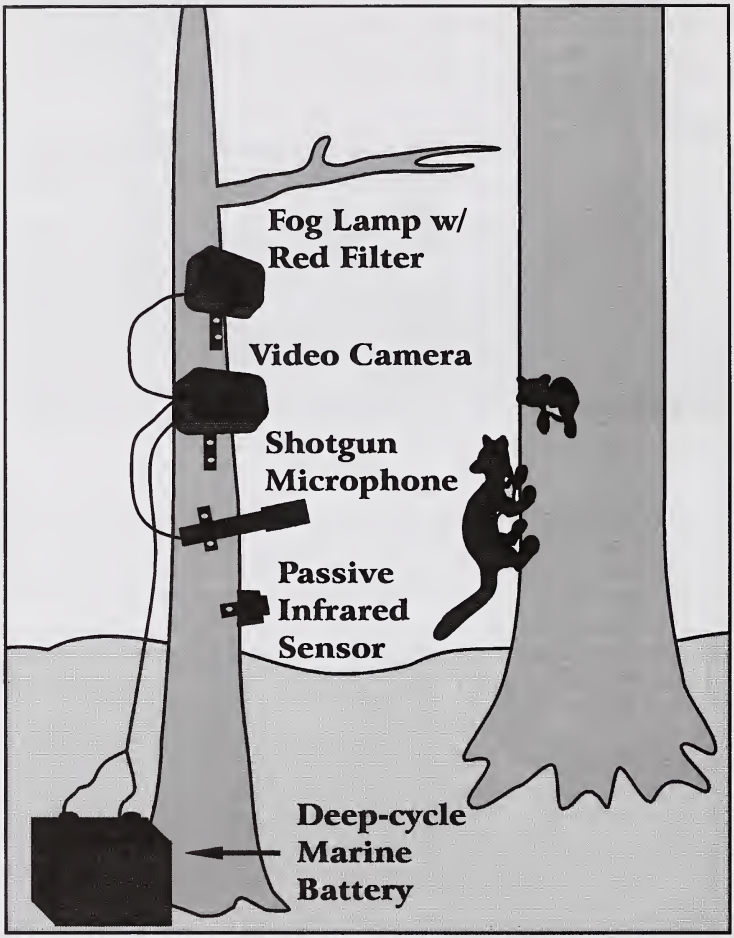

Figure 3. Video camera system mounted at a tree or snag den.

by either heat or motion (passive infrared type). The sensor was usually placed within 2 m of the entrance to minimize false activation. When tripped, the sensor sends a microwave signal to the receiver in the housing, and the video camera starts taping for a pre-programmed interval. We determined that 60-99 sec was optimal for our purposes. The system is fully integrated so that, when the infrared sensor is activated, the microphone and light engage. The red filter over the lamp presumably reduces visibility to martens. More than 1 transmitting sensor was sometimes used to ensure the camera was filming by time the animal entered the field of view. The camera was always aimed at the entrance of the cavity.

Each of the external monitoring cameras was checked every 1 to 4 days, depending on need and crew schedule. Film from the 35-mm cameras was usually checked after only a few exposures to ensure proper functioning of the camera. Subsequent batches were left in the camera until most of the film was exposed. Video tapes were reviewed in the field if the readout on the remote control indicated filming had occurred. When much of a tape had been used up, it was replaced with a new one. Unlike the 35-mm cameras, which could record a maximum of 36 exposures, the video camera could record up to 2 h of tape.

At the end of the denning season, all data were recorded on a log sheet. Each exposure from a 35-mm camera or video segment was considered to be a single event. We collected data on the camera and sensor types and numbers, the resting site number (individual number for all resting and den sites), exposure number, number of events in a series, date, time, disposition of the film, identity of the marten (male, female parent, other female, kit, unknown marten, and tag number when known), behavioral activities of the martens, other species, and prey. Radio-collared martens were identified by reflective tape on the transmitter case and collar. The age (kit vs. adult) of other animals was determined by physical appearance, and sexual characters helped to determine that some individuals were males. Kits were not marked, so individuals could not be recognized. Martens that could not be categorized into 1 of the above classes were considered unknowns. Due to time constraints, we only recorded 1 or 2 primary behavioral activities during the pilot study, but are compiling a list of behavioral attributes for future analysis.

Results

From May 1993 to early August 1995, we located 31 dens of 8 martens (Table 1). Kits were seen in 3 of the 6 dens we examined with the burrow camera. In 1 of the cases where no young were found, the kits had apparently been moved back to a previous site. In the other 2 cases where we did not find kits, we believe they were in the den, but beyond the reach of the probe. The 3 successfully

Table 1. Maternal dens of martens and types of camera systems used in this study. All dens are included, even if cameras were not deployed, to indicate dates of first use and den relocation patterns, as determined by radio telemetry.

Year	Marten	Den	Structure	Tree Species	Date of 1st Use[a]	Cameras[b]
1993	F01	1	live tree	ponderosa pine	05/26/93	S
		2	live tree	ponderosa pine	06/09/93	
	F02	1	live tree	ponderosa pine	05/11/93	
	F05	1	standing dead tree	lodgepole pine	05/17/93	S
		2	standing dead tree	lodgepole pine	05/19/93	S, (V)
1994	F01	1	standing dead tree	ponderosa pine	05/26/94	S
		2	fallen dead tree	ponderosa pine	06/29/94	S,V
	F05	1	slash pile		04/26/94	
		2	slash pile		06/02/94	S,V
		3	cut stump	unknown	08/10/94	S
	F12	1(?)	slash pile		06/27/94	
		2(?)	fallen dead tree	lodgepole pine	08/08/94	S
	F26	1	live tree	ponderosa pine	05/10/94	
		2	live tree	ponderosa pine	06/16/94	S
		3	slash pile		08/04/94	S
	F31	1	slash pile		05/10/94	
	F33	1	slash pile		05/18/94	S,V
1995	F01	1	standing dead tree	ponderosa pine	05/04/95	B
		2	standing dead tree	ponderosa pine	05/11/95	V
	F12	1	standing dead tree	lodgepole pine	05/15/95	
		2	fallen dead tree	lodgepole pine	05/30/95	B,S
		3	fallen dead tree	lodgepole pine	07/17/95	
	F26	1	fallen dead tree	lodgepole pine	05/15/95	B,S
		2	slash pile		07/17/95	
		3	slash pile		07/24/95	
	F33	1	fallen dead tree	lodgepole pine	05/16/95	B
		2	felled log	lodgepole pine	05/30/95	B,V

Table 1. Continued.

Year	Marten	Den	Structure	Tree Species	Date of 1st Use[a]	Cameras[b]
		3	slash pile		07/03/95	
		4	fallen dead tree	lodgepole pine	07/24/95	S
		5	slash pile		07/27/95	
	F47	1	fallen dead tree	lodgepole pine	05/24/95	B,V
		2	fallen dead tree	lodgepole pine	05/26/95	

[a] Date based on telemetry locations, when female was first found resting at this site.
[b] S = 35-mm still camera; V = video camera; B = burrow camera; (V) = video camera cursorily tested. Blank = no cameras used at site.

probed dens were all similar in structure. They were hollow lodgepole pine logs with numerous whorls of branch stobs and adjoining cavities. Bedding in the nest chamber was mostly chunks of rotten wood, but lichens and branches also were seen. Martens were never seen carrying bedding to the dens, so the origin of the materials is not known. In 2 of 3 instances, kits slept during probing, which usually lasted between 5 and 15 minutes (sometimes longer to obtain footage).

We recorded 2801 photographic events with 35-mm cameras (Table 2); only 19% (536) of the recorded events had a photograph of 1 or more martens (but it was 60% in 1995 because of selective placement and experience of the field crew establishing camera stations) and 7% (190) were of other species. The remaining 74% of the events were from accidental exposures, test firing, perceived motion (when the sensors move, rather than an object between them), and other factors. Accidental exposure was usually from wind, rain, and snow. Marten photographs were mostly of 1 or 2 kits (47%). The female parent was photographed less often (13%); both female and kit(s) appeared in the same event only 10% of the time. The proportion of events with a single unknown or unidentifiable marten was 19%. A total of 19 non-target species was photographed 190 times at dens with 35-mm cameras. Interestingly, 75% of those photographs were of species of squirrels (Sciuridae) that are frequently prey of martens (Martin 1994), including Douglas' squirrels *(Tamiasciurus douglasii*, 35%), golden-mantled ground squirrels (*Spermophilus lateralis*, 28%), chipmunks (*Tamias* spp., 9%), and northern flying squirrels *(Glaucomys sabrinus*, 1%) (the remaining 1% were identified only as sciurids or striped sciurids). Badgers (*Taxidea taxus*) were photographed on 7 occasions (4%) and a great horned owl (*Bubo virginianus*) was recorded once. These 2 species may be important predators of martens

Table 2. Summary of photographic events, showing different combinations of sexes and age classes at marten den sites. All adult females were believed to be parents. Unknown usually refers to a marten in a pose precluding identification. Unknown combination indicates more than 1 marten with at least 1 unidentifiable.

	1993	1994		1995	
	35-mm	35-mm	Video	35-mm	Video
Number of events (*n*)	834	1721	2030	246	753
Total events with martens (*n*)	94	294	340	148	178
Adult female only (%)	2	11	11	22	21
Adult male only (%)	9	9	7	11	3
Unknown only (%)	28	15	8	24	3
Kit(s) only (%)	56	62	54	11	44
Female + kit(s) (%)	6	3	21	28	28
Male adult + kits (%)	0	0	<1	0	0
Unknown combination (%)	1	0	0	4	1

in the area because carnivores and raptors are reported to kill martens (Strickland and Douglas 1987). Nine species of birds were recorded on the photographs.

We recorded 2783 events with video cameras (Table 2). Of these, 518 events (19%) were of 1 or more martens and 92 (3%) were of 6 other species. The percentage of non-animal events was similar to that for the 35-mm cameras (78%). Of events of martens, the proportions of kits (50%) and females (14%) was similar to 35-mm cameras; however, the percentage of female and kit(s) together was higher (23%). This discrepancy probably reflects the difference in duration of recording between the 2 camera types but is not independent of placement: only 4 of 18 (22%) of the dens had both types of cameras. Also, 35-mm cameras were usually placed at ground level sites (8 of 13, 62%) with the camera aimed at ground level, even when the dens were in trees or snags. Unknown or unidentifiable single martens accounted for only 6% of the events. As with 35-mm cameras, most (88 of 92, 96%) of the non-target species were squirrels, particularly Douglas' squirrels (69% of all non-target species events).

Of the 16 dens monitored from 1993-1995, 4 camera stations appeared to have been established after the female and kits had relocated to other dens; the remainder operated while the female and/or kits were at the den. Of the remaining dens with good data on date, females remained at the site from 1-71 days (n = 7 in

1994 and 1995, $\bar{x}$ = 21.4, SD = 23.9) after camera placement (Table 3). In only one situation did the female abandon the den within 1 week of camera placement. Similarly, kits at dens with good data for date remained from 2-64 days after camera placement (n = 8 in 1993-1995, $\bar{x}$ = 37.0, SD = 29.4). Thus, there was no immediate abandonment of den sites by martens (with only 1 possible exception). The fact that martens were frequently photographed exhibiting a wide array of behavioral attributes such as foraging, scent-marking, and playing would add credence to the notion that cameras had little influence on their behavior, with the following exceptions. The shutter and/or flash of the 35-mm cameras sometimes drew the attention of martens and the sensors or other equipment near a den were noticed. However, in the absence of noise, white light, or nearby equipment, the cameras seem fairly unintrusive. Burrow cameras, which did appear to be intrusive (especially when the female discovered us), never resulted in den abandonment.

Activity Patterns

We observed a shift in activity at the entrance of the dens across the duration of the denning season (Fig. 4). Our telemetry and live-trapping data suggest that

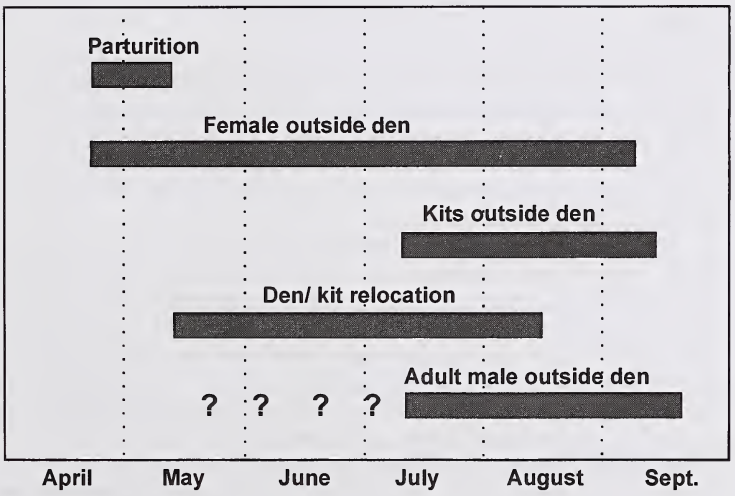

Figure 4. Generalized seasonal activity at maternal dens in the study area. This does not imply precise dates for all events, just general trends. The dates of first arrivals of males at dens is not well known.

parturition occurs in late April and early May. Typically, dens are first located during the first 2 weeks of May. Kits first appeared at den entrances during early July. As soon as they made their appearance they dominated photographic events, making frequent forays outside the entrance until they became independent, usually in late August to mid-September. According to our telemetry data, kits may be moved by the female almost anytime during the denning period (Table 1). Den relocation occurred during May, June, July, and August, but this was captured on tape only once. Adult males appeared most frequently after June, but this timing may be an artifact of establishing stations during the latter half of the denning period (Table 3).

Behavioral Observations

Kit Transfer: Telemetry data (Table 1) and audiovisual observations indicated that den relocation is typical behavior for martens in the study area. Of the 3 martens in Table 1 that did not select alternate sites, 1 was killed (on 13 July 1993) and the other 2 were believed to have lost their young. Den relocation was recorded on video tape on 30 June 1995, at 1042-1045 h, when a female (F47) was seen carrying her offspring from one den to another. Although the female was seen back at the former site the next day, the kits were not seen there until 6 July 1995. At this time, the kits were old enough to walk, but not yet fully coordinated.

Prey-related Activities: We recorded 22-24 sequences (temporally grouped events) involving prey, mostly on video. Except for 2 sequences with birds (dark-eyed junco, *Junco hyemalis*), all prey species were rodents, including golden-mantled ground squirrels, chipmunks, and mice. Identification of prey at the species level was difficult with cameras. In 2 sequences (8 and 24 August 1994) 2-3 prey items were seen at the den in 1 day. On 9 and 10 July 1994, F01 was seen giving mammalian prey to the kits.

Interactions with the Substrate and Equipment: Martens engaged in various activities involving the den structure. We documented martens scent-marking, scratching, and rolling on the structure. In some instances, the females rubbed their radio-collars. Martens were sometimes aware of the camera equipment in their vicinity. They usually paid no attention to video cameras but were aware of the sensors, if near the den, and of the 35-mm camera firing and its flash. At a den of F01 where a sensor was in the field of view of the video camera, a kit was recorded playing with the sensor's strap.

Males at the Den Site: The presence of adult males at dens was fairly common. We documented males at 6 of 16 dens (38%). In 1993, 2 males (M07 and M21) were documented at the entrance of the same den of F01 (at different times). In 1994, M21 was seen at 2 dens belonging to 2 females. The male and kits were only photographed in the same event on 1 occasion, 25 August 1994,

Table 3. Temporal relationship between den occupancy and monitoring by an established external camera. No detections (ND) probably reflect camera stations established after den relocation or (for F33 in 1994) kit loss. U = unknown dates.

Year	Marten #	Den #	Camera Date[a]	Prior Use[b]	Last Female[c]	Last Kit[d]
1993	F01	1	2 June	7	62	77
	F05	1	12 May	1	36	ND
		2	10 June	3	74	71
1994	F01	1	26 May	12	ND	ND
		2	29 June	1	71	64
	F05	2	24 May	-9	9	11
		3	10 August	6	30	32
	F26	1	10 May	27	ND	ND
		2	16 June	6	1	ND
	F33	1	18 May	20	9	ND
1995	F01	1	10 July	60	ND	ND
	F12	2	4 July	35	U	U
	F26	1	10 July	56	7	2
	F33	2	27 June	28	ND	ND
		3	25 July	22	U	16
	F47	1	27 June	34	23	23

[a] Date when first camera was established at den.

[b] Number of days that the female had been documented at the den prior to placement of cameras, as determined by radio telemetry. This number is not always an accurate assessment of true occupancy however, because martens were required to be resting at the site to document use. Thus, animals that were active outside the den were not included, making this measure conservative at times. A negative value indicates that the camera was established before use of the den was confirmed.

[c] In 1994-1995, number of days between camera establishment and the last detection of the female. In 1993, when a large percentage of adult collared martens were unidentifiable by 35-mm cameras (most or all adults were probably the female), this last detection was of a radio-collared adult.

[d] Number of days between camera establishment and the last detection of kits.

at 0718 h. On 24 August 1994, M21 was seen eating a striped sciurid only 11 minutes after a kit was seen carrying a striped sciurid, suggesting prey robbery. The female was never seen in the same event with the male.

In 1995, males were recorded at 4 of 6 dens with video or 35-mm cameras. On 20 July 1995, at 2058 h, a scrotal male (probably M29 or M34) was recorded scent-marking 5 times in 33 seconds at the entrance of a fallen-tree den of F47. It went just inside the den entrance once, but did not venture into the nest chamber. However, a male (probably M29 or M34) was seen entering the den cavity of F47 on 2 July 1995 on at least 3 occasions at 0959-1000 h. He scent-marked the entrance of the cavity twice. On 3 July 1995, at 2041 h, a male (probably M21) scent-marked at the end of a log den of F33, but did not enter the cavity.

Discussion

Techniques

Burrow Camera: To date, we have had little experience with the burrow camera, but it apparently will not be beneficial in all situations. This type of camera seems particularly well-suited for studies on ground burrows with limited branching, such as tortoise burrows (Spillers and Speake 1988). In the case of marten cavities, it is of limited value in tight situations where bending of the probe is frequent. However, for some sites, the burrow camera is a relatively quick and effective way to determine if a den is occupied by kits. It may be the most effective tool known to determine occupancy and possibly mortality from parturition until kits emerge from dens in July. The burrow camera also allowed us to view and characterize the internal structure of marten den cavities, something that is otherwise possible only by dissecting the structure. Details of the internal structure may give insight into denning structure selection.

One problem we found with the camera is that the semi-flexible sheath is not rigidly attached to the probe (it uses a small plastic coupler), so the probe can accidentally be dislodged when trying to retrieve it. To correct this problem, we secured the probe to the sheath with duct tape. In addition, for entering a large, straight cavity from the end, we found that attaching the sheath and probe to a wooden dowel was very effective. The resolution on the small video monitor of this camera is coarse. We recommend using a high resolution video camera (such as Hi-8) to record the image and then viewing the tape to search for kits. At 1 den, the kits were not seen on the burrow camera's monitor, but when the videotape was reviewed at the lab, 2 kits were seen on 2 separate occasions. Although the unit is hermetically sealed, snow and water on the lens obscure the view and frequent cleaning is necessary. The burrow camera is expensive (ca. $7,000 US, without tape recorder).

35-mm Camera: In general, these cameras function well, but we prefer the Olympus body to the Yashica for a variety of reasons. The mounting is less secure in the latter, it is not weather-resistant, it lacks a telephoto-wide angle dual lens setting, and it is more prone to false triggering. Unfortunately, camera models of commercially available monitoring systems change frequently so certain models cannot be specified. Because we often saw martens looking directly at the camera in photographs, we believe they sometimes looked up when the camera shutter and flash were triggered. The flash is mounted directly on the camera, making close-ups difficult, as that would put the flash and camera close to the subject. In addition, for our behavioral work, we found that these 35-mm cameras only record an instant view of behavior, making interpretation more subjective.

Video Camera: The video camera has a variety of beneficial features. It has a zoom lens, allowing the operator to place the camera away from the den (and out of reach of potential thieves), and it can be aimed at cavities in trees and snags. The camera operates on low light levels, minimizing the need for external lighting. The camera's use of a tape rather than roll of film offers 2 advantages. One is rapid feedback; the operator can review the tape in the field through the viewfinder and know if she/he is getting recordings rather than false activation and if the footage is important. The 35-mm camera requires that the film be taken in for processing, which can be quite time consuming in remote areas. By the time an error is noted (e.g., poor aim), a week or more may have elapsed with the problem uncorrected. The second advantage is that a tape can be re-used, although we recommend archiving all tapes that contain target-species photographs. One limitation of the video camera is its cost, which is approximately 8 times (with accessories) that of the commercially available 35-mm systems ($4000 *versus* $500 US).

Infrared Sensors: The most problematic mechanical feature of both the 35-mm and video systems is the infrared sensor. The passive types are more sensitive and prone to false activation because they will trigger in response to motion or a thermal change. The active infrared sensor requires a beam to be broken for a specified amount of time. To avoid false activation, the sensors, regardless of type, had to be mounted within about 2 m of the animal's path. Passive infrared sensors also had to be aimed at stable backgrounds to reduce false triggering. At dens monitored with video cameras, we usually had more than one passive sensor because there is about a 3-5 second time lag between triggering and filming. An increased number of sensors increases the chance of false triggering. Because of this threat, cameras should be checked fairly frequently (every 1-3 days). When a camera is falsely triggered, all of the film may be exposed because the source of the initial activation (e.g., blowing object or differentially heated background) tends to cause chronic reactivation. Although we used active sensors

with the 35-mm system and passive with the video system, both commercially available systems now come with either type of sensor. Each den is different, and an understanding of what the desired end results and mechanical limitations are is critical. Both sensors have their advantages and disadvantages and various arrays of one or both types may need to be evaluated. It is best to remember that the zone of activation for the passive system is an area, whereas the zone for the active system is a line.

An Overview of Den-monitoring Techniques and Systems: There have been no studies specifically addressing the internal structures of marten dens, so a comparison of methods is difficult. Before the use of burrow cameras, cavity viewing was usually accomplished using mirrors and flashlights (Speake and Altimere 1983). It is doubtful that detailed information could be gained from this technique. Another possible method to record internal structure would be den dissection. This method probably has some advantages over the use of burrow cameras. Internal structures, such as cavities, stobs, and bedding could be measured and quantified. However, there are some obvious limitations to this approach. Dissection could only be done on select structures after the resident animals had vacated. Poor structural integrity might preclude successful dissection. In addition, dissection of the den structure would remove it from the pool of available denning and resting sites. Without the aid of an exploratory device, kit confirmation can only be obtained when they are heard or seen, and they are seldom seen prior to their appearance outside the den entrance. By that time, the kits are already at least 10 weeks of age (Henry and Ruggiero 1993), and designation of previous sites as dens would be based on extensive radio telemetry and other evidence.

Our use of 2 types of camera systems to monitor the external area of the den allows us only a cursory comparison (Table 4) because the cameras were usually deployed differently. The ability to record lengthy visual sequences made video cameras superior to 35-mm cameras for recording behavioral traits and other specific information. For example, an observer is more likely to see and determine the species of prey a marten has in a 1-minute video clip than a 1/60 sec image on 35-mm film. However, 35-mm film has better resolution than video, so some details may be more distinguishable. We always used slide film so that images could be enlarged for study. Another major advantage of the video system's continual recording mode is that it is easier to decipher a sequence of events. For example, a female may return to a den with prey, give it to a kit, then leave the den. A 35-mm impression of this scenario would be incomplete—it might only capture the back of the female, leaving no clue as to what has occurred or the identity of the female. However, both types of cameras may fail to record events.

Table 4. A comparison of remotely automated external camera monitoring systems.

	35-mm Still Camera	Video Camera
Cost	ca. $500 US	ca. $4000 US
Maximum number of events	36	120 (@ 60 sec/event)
Frames per event	single	multiple
Mounting flexibility	lower	higher
Flash, noise disturbance	moderate-high	none-low
Telephoto capabilities	2 settings, no close-ups	ca. 10 × zoom
Film resolution	high	moderate
Sound recording	no	yes
Sequence deciphering	poor	good

If cameras are established long after the female and kits have been in residence, there is an increased risk that the martens will relocate their dens before much data can be collected. In our case, we sometimes established camera stations after martens had already left (Table 3). We likely encountered this problem because we spent time during the early denning period doing other activities (including telemetry verification at dens) and always waited for the female to be absent from the den. We recommend establishing stations 1-2 weeks after parturition at natal dens and immediately at post-natal dens.

Direct observation by field personnel would have certain advantages and disadvantages to cameras. With a camera, placement is always a trade-off. A close-up view offers some details, such as prey species and marten identification, whereas a more distant view offers others, such as den access. A human observer has a much greater field of view than a camera and can follow the animal's movement. In particular, 2 phenomena documented on camera were inconclusive: possible mating behavior associated with male presence and marten-prey interactions. It was not usually possible to determine whether the female brought kits food or if the kits captured prey themselves. Disadvantages include the cost of having a crew monitor a site for continual 24-h periods and possible influence of human presence. Also, observers have only 1 chance to make a subjective call on an event, whereas a video tape can be reviewed repeatedly and provides a permanent record for later verification.

It is difficult to accurately assess the degree of disturbance our cameras may have had on martens at dens, because martens frequently relocate to other den sites without the influence of cameras (Henry and Ruggiero 1993; Raphael and

Jones, this volume). With the exception of 1 female that abandoned its den within 1 week of camera placement, martens seem to exhibit strong site fidelity.

Denning Behavior

If the value of the recorded image is little more than capturing basic biology in action, then cameras are of limited use to conservation researchers. We found that the use of cameras complemented data from other sources to achieve a more complete understanding of how martens use their surroundings during the critical reproductive season. Once integrated, this knowledge will help land managers to make wise decisions about land use and retention of natural features. Burrow cameras, at least on occasion, offered rapid proof of kit occupancy and the characteristics of the internal den structure. Although the sample was small, all ground-level dens that were explored had features that offered protection from terrestrial predators (e.g., internal branch stobs and multiple chambers).

Using external monitoring cameras will allow us to determine activity patterns at the den and, with the aid of telemetry, the location of animals in relation to the structure and secondary den sites. Similarly, the seasonal use pattern can be chronicled in detail with cameras. We can gather data on major seasonal events such as kit appearance, weaning (from prey transfer), mobility, independence, and male appearance. The appearance of males at the den is an example of a previously unknown or little documented phenomenon that can be discovered using cameras; such an event may also have management implications. Henry and Ruggiero (1993) showed that copulation may occur in the proximity of kits, but the den site itself was not implicated as having any role. It seems likely that males are at dens to copulate, because they were seen to be scrotal and scent-marking at this time and it corresponds to the period of sexual activity (Enders and Leekley 1941, Jonkel and Weckwerth 1963, Henry and Raphael 1989, Henry and Ruggiero 1993). Males can readily find sexually mature females at maternal dens, so the following season's reproductive success may be linked to the den site. There is no evidence that the male contributes directly to the rearing of kits.

Biologists and land managers should be aware of these reproductively active times and plan human activities accordingly. Based on our camera work, den sites become very active in July at our study area. At this time the kits are apparently weaned and the female brings prey to the kits, possibly several times per day. Kits rapidly become more mobile in the first 2 weeks of July and begin to explore their surroundings. From July until some time in late August to mid-September the kits remain active at the den, slightly later than reported for martens in Wyoming by Henry and Ruggiero (1993). This period also coincides with the appearance of adult males, presumably on mating forays. These observations should not imply that the period of external den activity is more critical than the earlier period from parturition to weaning. Rather, they should imply

that there are different aspects of reproduction that must be considered when determining management strategies of martens and their habitats.

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USE OF REMOTE VIDEO CAMERAS FOR THE DETECTION OF FOREST CARNIVORES AND IN RADIO-TELEMETRY STUDIES OF FISHERS

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Abstract: Recent work on the development of survey techniques for forest carnivores describes the use of sooted tracking stations, snow tracking, and single-frame 35-mm and 110 camera systems, but not video systems. We experimented with both video and 35-mm remote camera stations in southwestern Oregon for use in surveys of forest carnivores and in radio-telemetry studies of fishers (*Martes pennanti*). Video systems were 8 times as expensive as 35-mm systems, but recorded more detections of fishers, detected more species of carnivores, had fewer problems, and enabled us to gather information on reproductive ecology and behavior. For these reasons, video systems offer many advantages over 35-mm systems. We describe improvements we made to a commercial video system and offer recommendations for establishing video camera stations in the field.

Introduction

A recent assessment of the conservation status of American marten (*Martes americana*), fisher (*M. pennanti*), lynx (*Lynx canadensis*), and wolverine (*Gulo*

gulo) in the western United States (Ruggiero et al. 1994) identified the need for more data on the distribution of all 4 species. Because of concern over loss of habitat and perceived extirpations of peripheral populations, 4 petitions have been submitted during the last 6 years to list fishers, lynx, and wolverines in the western United States under the Endangered Species Act (USDI Fish and Wildlife Service 1991, 1992, 1995, 1996). These concerns have generated renewed interest in developing reliable and cost-effective methods for conducting surveys to determine the presence of these and other forest carnivores.

Largely in response to these concerns, Zielinski and Kucera (1995) developed a manual that presents detailed descriptions of recommended techniques for surveying large areas to detect the presence of various species of small to medium-sized forest carnivores. Recommendations for the sampling effort necessary for reasonable certainty that a species is not present during the survey are also presented. The methods described in this manual include sooted track stations (see also Barrett 1983, Taylor and Raphael 1988), 35-mm and 110 remote camera stations (see also Jones and Raphael 1993, Kucera and Barrett 1993), and snow tracking (see also Thompson et al. 1981, Halfpenny 1987, Forrest 1988).

Recent advances in video technology have led to the development of remote video surveillance systems for use in wildlife research. Although remote video cameras are not discussed in detail by Zielinski and Kucera (1995), these systems offer many advantages over single-frame 35-mm and 110 remote camera systems. In this paper, we describe our experiences with remote video cameras to conduct surveys to detect the presence of forest carnivores, and to augment our radiotelemetry studies of fishers. In addition, we offer recommendations for modifying and using a commercial video surveillance system for such applications.

Preliminary Field Trials of a Commercial Video System

Winter 1993

During the winter of 1993, we conducted a survey to detect the presence of wolverines on the Rogue River National Forest in southwestern Oregon using remote video camera stations. The study area is located in the Mixed-Conifer Forest Zone, described by Franklin and Dyrness (1973) as a northern extension of the Sierra Nevada montane forest. This zone is characterized by highly dissected, mountainous terrain. During the course of this survey, recorded temperatures at bait stations ranged from -2° to 10°C.

We established 4 bait stations at elevations ranging from 1200 to 2000 m in accordance with procedures recommended by the USDA Forest Service (1991). We baited the stations with road-killed black-tailed deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) carcasses and congealed animal fat from a deep-fryer. To deter aerial scavengers, especially ravens (*Corvus corax*), we placed baits

under dense canopy cover. We checked the stations about once per week, replacing baits as needed. Between 1 January and 30 April 1993, we monitored each station with remote video cameras for 4-5 weeks. During this survey, we used the Compu-Tech™ model RM-680 video camera system as sold by the manufacturer (Compu-Tech Systems, Bend, Oregon 97708). The system consisted of a weatherproof housing, an 8-mm Sony™ video camera with 20X zoom capability, a PIR-12 dual-sensor transmitter/receiver for activating the camera system, and an EM-100 external microphone. No artificial lights were used during this survey.

During preliminary surveys in the winters of 1993 and 1994, we configured the remote video stations according to the general operating instructions provided by Compu-Tech. As we gained experience with the system during field applications, we began experimenting with various modifications to this configuration. We set the timer on the unit to record for 35 seconds once activated. This interval worked well to minimize the amount of tape wasted on nontarget species but still provide sufficient footage to identify target species. To increase the likelihood that weasels (*Mustela* spp.) and other small forest carnivores would be detected, we set the sensitivity of the sensors at maximum.

Results were disappointing; we obtained only 1 video sequence of 2 martens at a bait station. We defined a video sequence as any camera activation (35-second recording interval) in which a species could be positively identified. If an animal remained at the bait for more than 35 seconds and reactivated the camera, or was detected removing pieces of bait from the bait pile in successive video segments, these segments were treated as 1 video sequence. The low number of detections was attributable to several problems: ravens frequently activated the sensors once they found the bait, blowing snow often covered the camera lens, and cold temperatures quickly drained the internal lead acid batteries that operate the cameras. Because of the low temperatures we encountered in our study area, and the frequency with which ravens and other birds activated the system, the internal batteries were often depleted in only a few days.

Winter 1994

From 6 December 1993 to 22 March 1994, we maintained 28 bait stations at locations varying in elevation from 750 to 1893 m. Temperatures recorded at the stations ranged from -5° to 18°C. For bait, we used unplucked chickens, whole salmon (*Oncorhynchus* spp.) and steelhead (*Oncorhynchus mykiss gairdneri*) and, occasionally, road-killed deer. At any one time, 9 of the bait stations were monitored with remote cameras (3 with 35-mm Trailmaster™ 1500 cameras [Kucera and Barrett 1993], and 6 with remote video systems). The other 19 stations were monitored opportunistically for the presence of carnivore tracks. If mustelid tracks were found, we moved one of the cameras to that site to obtain a

photographic record. During this survey, we experimented with a variety of camera and bait station configurations for both video and 35-mm cameras. In general, our configurations for video stations were similar to that described for dual-sensor cameras by Kucera et al. (1995); for 35-mm stations, our configuration was similar to that described for single-sensor cameras (Kucera et al. 1995). The primary difference from these configurations is that we generally piled bait on the ground, rather than wiring it to a tree or hanging it between 2 trees, and aimed the sensor beams directly over the top of the bait pile.

We recorded 18 video sequences of fishers at 3 stations at elevations ranging from 1097-1219 m, and 5 sequences of martens at 1 station at 1646 m. We obtained 2 35-mm photos of fishers at 1 station at 1100 m elevation, and 1 of a marten at 1628 m. Although we encountered technical problems with both the video and 35-mm systems, the Trailmaster 1500 systems were more troublesome than the video systems. We encountered the following problems with the 35-mm systems: 1 camera that failed to operate, requiring repairs by the manufacturer; condensation on the lens of the camera resulting in blurry images; moisture collecting at the plug on the cable connecting the receiver to the camera, causing the camera to expose the entire roll of film; several instances in which corrosion built up on the cable connection rendering the cable unusable; small mammals deactivating the system by chewing through the cable; and misalignment of the camera due to failure of the ball-and-socket joint on the camera tripod mount following the accumulation of snow or animals landing on the unit. This latter problem occurred with all units; without modifications, the mounting system will not function reliably. Kucera et al. (1995) offered suggestions for improving the security of these mounts by using duct tape or replacing the mount with an L-shaped metal bracket and a larger ball and socket joint.

Because we experimented with various modifications to the video system during the 1994 survey and were just beginning to use the 35-mm Trailmaster system, comparison of results obtained with each system during the second year of the study are not appropriate. However, this survey enabled us to become familiar with the operation and configuration of the 35-mm cameras systems and to further refine our video system to improve performance.

Modifications to the Video System

Battery

To increase the battery life of the system, we added an external, heavy-duty, deep-cycle 12-volt marine battery that we placed in a polyurethane ice chest. In areas with sufficient snow, the ice chest can be buried in the snow to provide additional insulation. We ran the battery wires through the drain plug in the ice chest. With this configuration, the battery will last long enough to record the

entire length of videotape under typical winter conditions. With any remote sampling device involving electronic equipment, however, there are many potential problems. To minimize wasted sampling effort, we checked the cameras on a weekly basis.

Lighting System

To obtain video detections at night, we tried various illumination systems. We began by using the KR-70 nocturnal lighting system supplied by Compu-Tech. This lighting system consists of a krypton flashlight mounted on top of the camera unit. This light proved to be unsatisfactory, providing relatively low illumination and a narrow field of view. Animals detected at night in the lighted portions of the video image were difficult to identify to species and the peripheral portions of the image were dark. Often, the camera was activated at night but nothing was visible in the field of view, suggesting that animals were present outside the illuminated area.

To increase illumination and widen the field of view on the video image during nighttime exposures, we replaced the KR-70 lighting system with 12-volt flood, spot, or fog lamps designed for external use on off-road vehicles (ORVs). Flood lamps (either 55 or 100 W) worked best, illuminating the entire field of view. We placed the lamp in a rectangular plywood housing to protect it from weather and falling debris. The wires ran through a hole in the bottom of the housing. To maximize the illuminated field, we mounted the unit on a tree either next to the camera or directly above it, and aimed the lamp directly at the bait.

To evaluate whether forest carnivores would be deterred from remaining at the stations with the bright, white light from the ORV flood lamps, we compared detections and behaviors of carnivores obtained at a camera station with a red glass filter to those obtained at the same site, but with no filter. Trials were conducted at 2 sites in the winter of 1994 at elevations of 1085 and 1311 m. The first site was monitored from 1 March to 14 April, with recorded temperatures at the bait stations ranging from 4° to 7°C. We detected snowshoe hare (*Lepus americanus*), western spotted skunk (*Spilogale gracilis*), marten, and elk. The second site was monitored from 7 March to 14 April, with recorded temperatures of 0° to 5°C. Species detected at this site included fisher, coyote (*Canis latrans*), and northern flying squirrel *(Glaucomys sabrinus*). We evaluated animal reactions to the white light by subjectively comparing behaviors recorded at video stations with red lights to those at stations with white lights. Although coyotes reacted to both red and white light, we could discern no obvious reaction or aversion to the white light by other species of carnivores. Consequently, we used the flood lamps without a red filter at all subsequent camera stations.

To configure the video systems in the field, we recommend setting video cameras 5-10 m from the bait (Fig. 1). This provides the best compromise between

maximizing the field of view and discerning details in the video image. We placed the camera system about 1.5 m from the ground, pointing slightly downward to reduce glare and obstruction of the lens by rain or blowing snow. After the sensor is activated, there is a minimum delay of 2 seconds before the system turns the lights and camera on, and an additional 3-second delay before the video camera begins recording an image. This results in a minimum delay of 5 seconds after an animal enters the range of the sensors before the camera begins recording. If the field of view is too small, an animal that is not going to the bait may move out of range before the camera starts recording. We found that adding a second sensor to the system and crossing the beams over the bait to increase the area covered by the sensors helped to reduce the frequency of blank footage. In addition, because animals may leave the bait station immediately after the lights come on and not be recorded on tape, the lighting system should be re-configured so that the light is turned on after the camera begins recording.

Comparison of the Modified Video System with the 35-mm System

In the winter of 1995, we designed our survey according to recommendations provided by Zielinski et al. (1995). Their protocol specifies a minimum of 2 cameras set in each 10.4 km^2 sample unit (4 1-mi^2 sections arranged in a square) and placed 0.8 to 1.6 km apart. We surveyed 15 sample units with both video and 35-mm remote cameras from 4 January to 14 April 1995. In each sample unit, cameras were operated until a fisher detection was made or for a total of 30 days, whichever came first. Stations were baited with unplucked chickens, fish, and occasionally, beaver (*Castor canadensis*) meat or deer carcasses. In each sample unit, we set 1 video system and 1 35-mm Trailmaster 1500 system at least 1 km apart. Within each sample unit, video and 35-mm stations were baited identically. Thus, sampling effort in 1995 was equivalent for video and 35-mm cameras. We configured the 35-mm camera stations as recommended by Kucera et al. (1995), set the sensitivity of the sensor at maximum, and programmed a 2-minute delay between photos. We generally placed the camera above the receiver so that the entire infrared beam was in the photo frame. Video stations were configured as shown in Figure 1 with the sensitivity of the sensor set at maximum and the sequence length set at 35 seconds.

Video cameras detected almost twice as many carnivore species during this survey than 35-mm cameras. We recorded 11 species with video cameras: cougar *(Felis concolor)*, bobcat (*Lynx rufus*), coyote, raccoon (*Procyon lotor*), ringtail *(Bassariscus astutus)*, fisher, marten, striped skunk (*Mephitis mephitis*), spotted skunk, long-tailed weasel (*Mustela frenata*), and ermine *(M. erminea)*, and only 6 with 35-mm cameras: bobcat, coyote, raccoon, fisher, marten, and spotted skunk. Although the number of fisher detections was low with both types

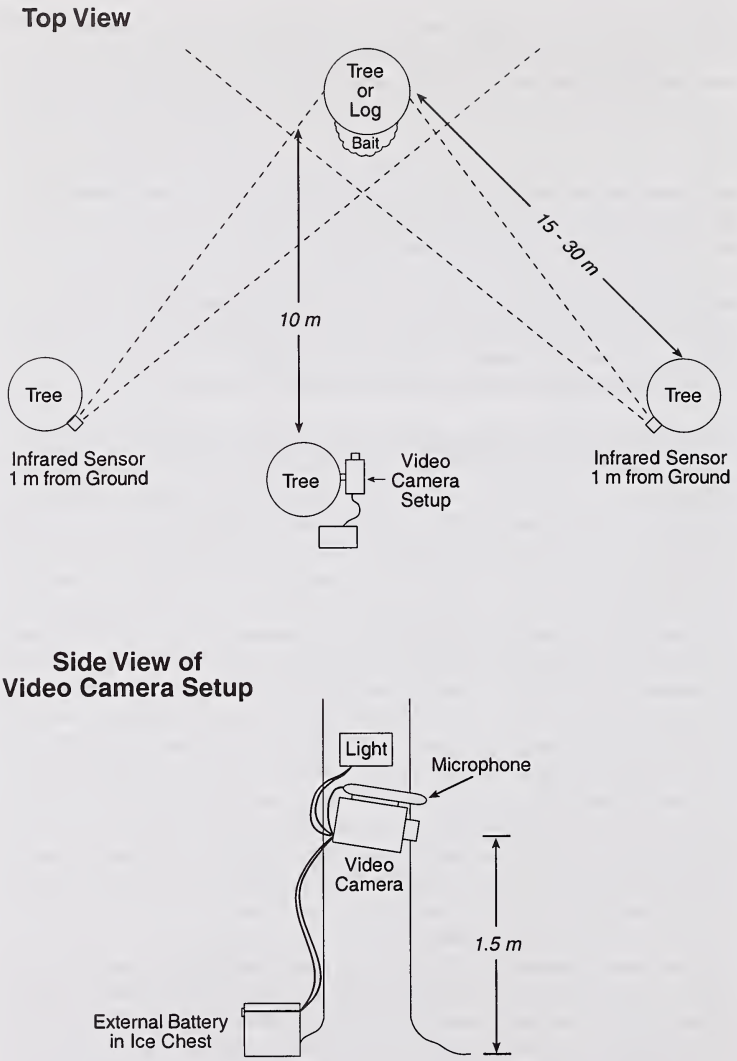

Figure 1. Remote video camera system for monitoring forest carnivores.

of cameras, we obtained twice as many with video (4/15 sample units) than with 35-mm cameras (2/15 sample units). Video cameras also recorded a marten scent-marking, and interactions at a carcass between a bobcat and coyote, cougar and spotted skunk, and raccoon and spotted skunk.

There are several possible explanations for the higher number of video detections. We had fewer technical problems with video stations compared to 35-mm stations, which resulted in more sampling opportunities with video cameras. In addition, with the auxiliary lighting system on the video cameras, a larger area was illuminated than is provided by the flash units on the 35-mm cameras. Another advantage of video cameras is that videotape does not need to be developed; consequently, determining if a target species has been detected and relocating the station to another sample unit can occur more rapidly than with 35-mm cameras. This could increase the efficiency of camera surveys by enabling more units to be surveyed during the sampling period.

Use of Video Cameras in Radio-Telemetry Studies of Fishers

We initiated a radio-telemetry study of fishers in this area in March 1995 using information gained from both video and 35-mm cameras to locate trapsites. Because video detections are often several minutes long, the probability of discerning individual characteristics such as sex, size, and pelage coloration, especially ventral blazes, is greater than with other remote detection systems. This facilitates the allocation of trapping effort, particularly if one wishes to target a subset of the study population such as males, females, or females with kits. In addition, we glued reflective tape of different colors onto the anterior surfaces of our radio-transmitters and eartags. With this tape in place, study animals can often be identified when detected by video cameras.

One of the most useful attributes of remote video cameras is their ability to gather information on reproductive performance and den use. During June 1995, we used video cameras to monitor 2 logs used as maternal dens by one of our study animals. We set up the video cameras about 10 m from the end of the logs, placing 2 sensors 8-10 m away aimed at right angles to each other to cross at the den opening. We set the sensitivity of the sensor at maximum and the recording time per activation at 3 min. To minimize disturbance to the female and kits, we did not use an external lighting system. The video cameras provided a simple and unobtrusive means of assessing reproductive performance; we were able to determine from the video footage that she had 2 kits. In addition, many morphological details and behavior patterns could be determined from the video footage. For example, we estimated that the kits were born in the last week of March, based on their agility on the den logs and their size relative to the female.

There was no indication from her behavior that the presence of the video cameras caused her to move the kits prematurely. Initially, she carefully investigated the immediate vicinity of the den site, including looking directly at the camera, but in subsequent footage paid no attention to the camera. Had she been significantly disturbed by the presence of the video station, it is likely she would have moved the kits immediately.

We tracked this same female during March 1996, and determined that she was repeatedly using a decadent tree containing several pileated woodpecker (*Dryocopus pileatus*) holes 9-18 m from the ground. We monitored her for several more weeks to verify that this tree was a natal den and to avoid any disturbance during the birthing period. On 23 April, after the female had left the area to forage, we set up a video camera approximately 40 m from the tree and focused it on the hole we suspected she was using. We eliminated the external battery as well as the lighting system and placed the camera station in the opposite direction from where she generally traveled after leaving the site to minimize the chance of her discovering the station. We placed 2 infrared sensors about 20 m from the structure at right angles to each other with the detection areas focused at the base of the tree about 0.5 m from the ground. With this configuration, the entire circumference of the tree was covered, and by the time she got to the cavity, the camera would be recording.

We checked the camera 4 days later. The video footage showed that she was climbing past the cavity we thought she was using and going around to the opposite side of the tree. We aimed the first camera at the base of tree and set up a second video camera 40 m from the tree aimed at cavities on the opposite side. We set up another sensor at the second camera about 30 m from the den tree and focused its detection area on the cavities to document her departures from the den. All sensors were configured to trigger both cameras. Using remote video cameras, we were able to determine which cavity she was using without risk of den abandonment from the disturbance our presence might have caused while she was at the den. For these and many other potential applications, remote video cameras offer wildlife researchers unprecedented opportunities to study fisher reproductive ecology and behavior during radio-telemetry studies.

It is important to realize, however, that these kinds of research activities are potentially disruptive to the animals under study. Females are more energetically stressed and probably more sensitive to disturbance during denning than at other times of the year. In addition, suitable den sites may be limited in availability, and moving kits to suboptimal sites could negatively affect reproductive performance. Consequently, any activities that may cause females to abandon natal or maternal dens and move kits to alternate sites must be conducted with caution. There is little information available to evaluate the potential effects of monitoring den sites with remote video cameras. Our experiences indicate,

however, that female fishers will tolerate their presence. Although kits were moved from both maternal dens we monitored in 1995 within a week of establishing the cameras, neither den was abandoned immediately. In 4/5 instances when Paragi (1990) handled kits in Maine, they were moved to another den within 24 hours. Furthermore, we monitored the dens during the latter part of the 8-12 week denning period (Paragi 1990, Arthur and Krohn 1991) which is when maternal dens are beginning to be abandoned, in any case. Jones et al. (this volume) monitored 13 maternal dens of martens with remote video cameras from 1994-1995; in only 1 instance did the female immediately relocate the den to another site. At all other dens, the average length of time females occupied the den after camera establishment was 21.4 days, with a range of 7-71 days. At the natal den we monitored in 1996, we were extremely cautious in our activities near the den site and monitored the den with remote video cameras for 31 days without any evidence of disturbance to the female.

We recommend the following procedures to ensure that disturbance at dens is minimized. Do not approach a den or set up a camera until the female leaves the area. Do not use artificial lighting systems to illuminate the scene. If possible, set up cameras in the opposite direction from which the female leaves the vicinity of the den site. Set cameras and sensors at least 20 m from the den structure. Minimize the number of people involved in establishing the camera station and, to the extent possible, avoid human activity in the immediate vicinity of the den.

Conclusions

The cost of our modified video systems is about 8 times that of the Trailmaster 1500 35-mm system (about $5000 *versus* $600 US), but there are many advantages to the video system that may justify the additional expense. Although our sample sizes were small, we were more successful at obtaining photographic detections of fishers and detected almost twice as many species of carnivores with the video system than with the 35-mm system. In addition, we experienced far fewer technical problems with the video system, which may have been a factor in their relative performance. Because of frequent problems, the 35-mm systems need to be checked more often than the video systems, which adds significantly to the cost of using them. Lastly, video cameras enable researchers to gather behavioral data that cannot be obtained with single-frame cameras. In addition to monitoring den sites, video cameras can be used to study the behavior of target species at 35-mm camera stations, sooted track stations, or trapsites to gain insights into how such devices might be modified or deployed differently to improve their performance.

Acknowledgments

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IMPROVED TRAPPING STANDARDS FOR MARTEN AND FISHER

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Abstract: Research to develop traps that can render furbearers rapidly (≤3 min) unconscious indicated that only a few traps could effectively kill American martens (*Martes americana*) and fishers (*Martes pennanti*). The C120 Magnum rotating-jaw trap (mean momentum = 1.09 kg m/sec, minimum clamping force = 254 Newtons [N]), the Kania planar trap (1.75 kg m/sec and 210 N), and the Bionic mousetrap (5.00 kg m/sec and 50 N, tested with the anatomically stronger mink [*Mustela vison*]) have the ability to render martens irreversibly unconscious in ≤3 min. The mean momentum and minimum clamping forces of these traps were used to generate a regression line (kill threshold) to estimate the lowest levels of energy required to effectively kill martens. Data on traps that failed to render martens unconscious in ≤3 min suggested that an effective marten trap must have a mean momentum ≥1 kg m/sec. According to the resulting kill threshold line, minimum clamping forces may range from 49 N, for a 5 kg m/sec momentum, to 254 N, for a 1 kg m/sec momentum. This kill threshold line is markedly different from that reported in the Canadian General Standards Board's 1984 standards where marten traps have a momentum ranging from 0 to 2.6 kg m/sec and corresponding minimum clamping forces ranging from 448 to 0 N. Only the Bionic trap was found effective for killing fishers. The mean momentum and maximum clamping forces of traps that failed to render fishers unconscious in ≤3 min were used to generate a regression line to determine levels of energy that are insufficient to effectively kill fishers. However, data are lacking to ascertain the levels of energy necessary to consistently render fishers unconscious in ≤3 min. Canadian trapping standards should be updated to reflect technological progress. The C120 Magnum and the Kania traps have been manufactured for many years; marten traps that do not meet upgraded standards should be removed from the market. Killing traps commonly used to harvest fishers are ineffective and the Bionic mousetrap is still not manufactured. Box traps are therefore the only trapping devices that can presently ensure the humane capture of fishers.

Introduction

Public concerns regarding the welfare of trapped animals are valid. If trapping of American martens (*Martes americana*) and fishers (*Martes pennanti*) is to continue, it must incorporate more effective (humane) trapping technology (Proulx and Barrett 1994). This new technology must also be included in

standards where criteria permit one to recognize acceptable traps. Canada is the only country with established national standards (Canadian General Standards Board [CGSB] 1984) for specification and performance of killing-type traps (Barrett et al. 1988). These standards were submitted to the technical committee of the International Organization for Standardization for consideration and possible adoption internationally (Jotham 1992). From 1985 to 1993, extensive research was carried out on killing traps (Proulx 1993). In the light of this research, this paper intends to assess the suitability of Canadian standards for the selection of traps to harvest marten and fisher.

The Canadian Standards

The CGSB's (1984) killing-trap standards incorporated the Federal Provincial Committee for Humane Trapping's (FPCHT 1981) kill thresholds, which are the lowest energy levels necessary to render animals unconscious within a 3-minute period. These thresholds were achieved by subjecting anesthetized animals to various levels of impact and/or clamping forces (FPCHT 1981). According to size and species characteristics, FPCHT (1981) established animal groupings. Marten was pooled with muskrat (*Ondatra zibethicus*) and mink (*Mustela vison*). Fisher was placed in another group with raccoon (*Procyon lotor*). For each group, a threshold line establishing a linear relationship between the minimum striking and clamping forces was established (FPCHT 1981; Figs. 1, 2).

A trap is considered to have the potential to render martens irreversibly unconscious in ≤3 min if it rates above a line defined by CGSB (1984):

$$p \geq 2.6 - 0.0058\,F$$

where p = momentum (kg m/sec), and F = clamping force (Newtons [N]). Therefore, such a trap would have a momentum ranging from 0 to 2.6 kg m/sec and corresponding clamping forces ranging from 448 to 0 N (Fig. 1).

A trap for fishers must rate above the following line (CGSB 1984):

$$p \geq 9.3 - 0.027\,F$$

where momentum values range from 0 to 9.3 kg m/sec and corresponding clamping forces, from 344 to 0 N (Fig. 2).

Trap Testing and Kill Threshold Development

Proulx and Barrett (1994) defined an effective killing trap as a device that has the potential, at a 95% confidence level, to render ≥70% of target animals

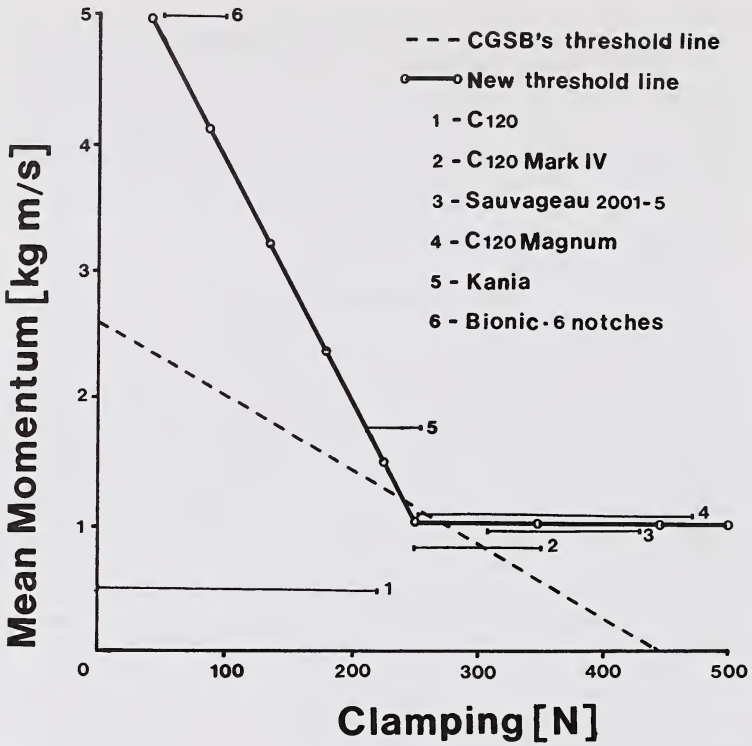

Figure 1. Marten kill threshold lines recommended by CGSB (1984) and this study, and the performance of the traps tested.

irreversibly unconscious in ≤3 min. Their scientific evaluation consisted of a series of sequential steps in simulated natural environments and on traplines (Proulx and Barrett 1991a). Traps were mechanically evaluated (Cook and Proulx 1989a,b) and their average momentum and clamping forces at different jaw openings plotted against CGSB's (1984) marten and fisher kill threshold lines.

Marten

Trap Testing: Rotating-jaw traps are frequently used to harvest martens. They consist of 2 wire frames (12.9 × 12.9 cm) hinged at their centerpoint to operate

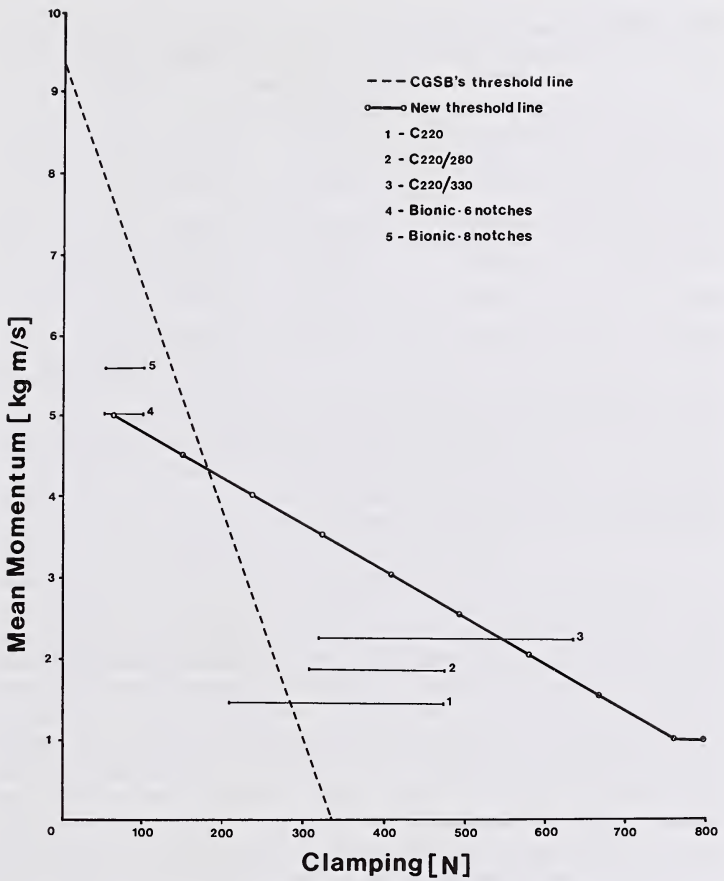

Figure 2. Fisher kill threshold lines recommended by CGSB (1984) and this study, and the performance of the traps tested.

in a scissor-like action powered by 2 torsion springs. Four models were thoroughly studied: the Conibear 120 (Woodstream Corp., Lititz, Pennsylvania), the C120 Mark IV (an experimental prototype), the C120 Magnum, and the Sauvageau 2001-5 traps (Les Pièges du Québec Enr., St. Hyacinthe, Quebec).

Table 1. Mean momentum and clamping forces of marten traps.

Trap	Momentum (kg m/sec)	Range of clamping forces (N)[a]	Reference
Conibear 120	0.538[b]	0-224	Cook and Proulx (1989b)
C120 Mark IV	0.811[b]	254-353	Cook and Proulx (1989b)
Sauvageau 2001-5	0.940[b]	310-430	Proulx (1990)
C120 Magnum	1.090[b]	254-473	Proulx et al. (1989a)
Kania	1.750[c]	210-255	Proulx (1990)
Bionic[d]	5.000[e]	50-100	FPCHT (1981)
			Proulx and Barrett (1993a)

[a] Clamping forces for trap jaw openings ranging from 5 to 40 mm (N = newtons).
[b] Determined at one half the total displacement from trip position of 1 closing jaw.
[c] Determined at 6 cm displacement of closing jaw.
[d] Spring wound up at 6 notches (Proulx and Barrett 1991b).
[e] Determined at 40-cm displacement of closing jaw.

The Conibear 120 is the most commonly used trap to harvest martens (Proulx et al. 1989b). It has low energy levels (Table 1), and it rates below the kill threshold line at all openings (Fig. 1). According to this rating, this trap does not have the potential to consistently render a marten unconscious in ≤3 min. This evaluation was confirmed by Proulx et al.'s (1989b) work on martens in simulated natural environments.

The C120 Mark IV consists of a Conibear 120 frame with shortened Conibear 126 (Woodstream Corp., Lititz, Pennsylvania) springs and 2 clamping bars welded to the same frame (Cook and Proulx 1989b). Its mean momentum and clamping forces are greater than those of the Conibear 120 (Table 1) and its position on the threshold graph overlapped the kill threshold line (Fig. 1). The C120 Mark IV was found to be a more effective killing trap than the Conibear 120 (Proulx et al. 1989b) but it is unlikely that it would consistently render martens unconscious in ≤3 min (Proulx et al. 1989a).

Proulx et al. (1989a) upgraded the C120 Mark IV to a C120 Magnum (Table 1) which rated above the CGSB's (1984) kill threshold line (Fig. 1). The C120 Magnum met the research criteria and consistently rendered martens unconscious in ≤3 min.

The Sauvageau 2001-5 is a modified Conibear 120 with an extra bar welded on the striking jaws of 1 trap frame. The trap has a mean momentum slightly lower than that of the C120 Magnum, but it still rates above the CGSB's (1984)

kill threshold line (Fig. 1). Although it had the potential to be an effective killing trap, tests in simulated natural environments showed that it could not consistently render a marten unconscious in ≤3 min (Proulx 1990).

Proulx (1990) also reported findings on the Kania (E. Kania, Winlaw, B.C.), a planar trap where 1 arm of the coil spring is used as a striking bar. This trap had a mean momentum markedly higher than those of the rotating-jaw traps and clamping forces between those recorded with the Conibear 120 and the C120 Mark IV (Table 1). On the threshold graph, the trap rated above the kill threshold line (Fig. 1), and Proulx (1990) found that it had the potential to consistently render martens unconscious in ≤3 min.

Finally, the Bionic trap (W. Gabry, Vavenby, B.C.) is also a device that has the potential to effectively kill martens. The trap has an exceptionally high mean momentum (Table 1) when its spring is wound up to 6 notches, and it can effectively kill mink, a species that is anatomically stronger than marten and is not consistently rendered unconscious in ≤3 min by a single strike of the C120 Magnum (Proulx et al. 1990, Proulx and Barrett 1991b).

New Kill Threshold: The C120 Magnum, the Kania and the Bionic traps are 3 trapping devices that can consistently render martens unconscious in ≤3 min. Using their mean momentum and minimum clamping forces, a new kill threshold line can be determined with the following equation:

$$p \geq 5.95 - 0.0195\,F$$

However, kill tests in simulated natural environments also showed that the C120 Mark IV and the Sauvageau 2001-5 traps failed to consistently render martens unconscious in ≤3 min, despite their relatively high clamping forces (Table 1). These 2 traps and all the others that did not meet the research criteria, had a mean momentum ≤1 kg m/sec. This observation suggests that the kill threshold line should be truncated to eliminate mean momentum values < 1 kg m/sec. Also, because captured animals may struggle and pull out of a trap (Proulx and Barrett 1993a), traps with high momentum values, but no clamping force, are not considered as potentially effective killing traps. According to the resulting kill threshold line, minimum clamping forces may range from 42 N for a momentum of 5 kg m/sec to 254 N for a momentum of 1 kg m/sec (Fig. 1). Traps that overlap or rate above the kill threshold line may have the potential to effectively kill martens.

Fisher

Trap Testing: The Conibear 220 (Woodstream Corp. Lititz, Pennsylvania) is commonly used to harvest fishers (Currie and Robertson 1992). However,

Table 2. Mean momentum and clamping forces of fisher traps.

Trap	Momentum (kg m/sec)	Range of clamping forces (N)[a]	Reference
Conibear 220	1.450[b]	206-472	Proulx and Barrett (1993b)
C220/280	1.904[b]	306-474	Proulx and Barrett (1993b)
C220/330	2.253[b]	317-633	Proulx and Barrett (1993b)
Bionic[c]	5.000[d]	50-100	FPCHT (1981)
			Proulx and Barrett (1993a)

[a] Clamping forces for trap jaw openings ranging from 10 to 80 mm (N = newtons).

[b] Determined at one half the total displacement from trip position of 1 closing jaw.

[c] Spring wound up at 6 notches (Proulx and Barrett 1993b).

[d] Determined at 40-cm displacement of closing jaw.

FPCHT (1981) suggested that this trap did not generate sufficient energy to effectively kill fishers.

The C220/280 trap is a modified Conibear 220 with 4 clamping bars welded to the striking jaws and Conibear 280 (Woodstream Corp., Lititz, Pennsylvania) springs. It generates high energy levels (Table 2) and rates above CGSB's (1984) kill threshold line (Fig. 2). Proulx and Barrett (1993b) tested this trap with fishers immobilized with ketamine and concluded that it may not have the potential to effectively kill unanesthetized animals. For this reason, they produced the C220/330 trap, which has clamping bars and Conibear 330 (Woodstream Corp., Lititz, Pennsylvania) springs. This trap has very high mean momentum and clamping forces (Table 2) and rates above CGSB's (1984) kill threshold line (Fig. 2). However, Proulx and Barrett (1993b) showed that it did not have the potential to effectively kill fishers.

When the Bionic trap was cocked at 6 notches (5 kg m/sec, set to kill a mink), the trap rated below CGSB's (1984) kill threshold line and was found ineffective in animal-based studies (Proulx and Barrett 1993a). When wound up to 8 notches, the trap had a mean momentum of 5.6 kg m/sec. Although the trap rated below the kill threshold line (Fig. 2), it consistently rendered fishers irreversibly unconscious in ≤3 min.

New Kill Threshold: Only the Bionic trap was found effective for killing fishers, so a kill threshold line based on the momentum and minimum clamping forces of a series of successful fisher traps cannot be established. However, using the average momentum and the maximum clamping forces of traps that failed the animal-based studies, one can determine a kill threshold line where traps

overlapping or rating below it do not have the potential to effectively kill fishers. This threshold line can be determined with the following equation:

$$p > 5.35 - 0.0057\,F$$

According to the information gathered with martens, this kill threshold line should also be truncated to eliminate traps with a mean momentum <1 kg m/sec (Fig. 2). Effective killing traps must rate above the kill threshold line. More animal-based data with different trap models are required to ascertain the levels of energy necessary to consistently render fishers unconscious in ≤3 min.

Discussion

This study shows that CGSB's (1984) standards are inadequate for identifying traps that effectively kill martens and fishers. Based on the new kill threshold values, marten and fisher traps must have markedly greater mean momentum and clamping forces than those accepted in the past. Furthermore, traps with a mean momentum value < 1 kg m/sec, or without clamping power, are no longer eligible for testing.

Although new kill threshold lines for marten and fisher are more discriminating than those of CGSB (1984), their use in the selection of potentially effective killing traps differs. In the case of marten, the kill threshold line was developed with traps that had been found effective in animal-based studies. Therefore, it is likely that traps that generate energy levels equal or higher than those previously tested traps will also be found effective as long as they strike the animals in the same vital regions as those reported by Proulx et al. (1989a, 1990). However, this kill threshold line was developed with a small data set and more animal-based studies with potential killing traps should be conducted to further ascertain their positions on the kill threshold graph. These studies should not be restricted to animals that have been immobilized by a dissociative anesthetic and whose muscles offer less resistance to the striking bars. They should involve unanesthetized animals that are aware of their capture and are able to "fight" the trap (Proulx et al. 1989b).

In the case of fisher, the kill threshold line was developed with traps that had failed the animal-based studies. Therefore, traps with energy levels that are identical or lower than those of previously tested traps are likely to fail. Such traps should not be eligible for animal-based studies. Only traps that rate above the kill threshold line should be considered for such studies.

Management Implications

Proulx and Barrett (1994) pointed out that if marten and fisher trapping is to continue in North America, trap technology must evolve with public sentiments and meet the challenges of effective trapping and conservation. The new kill threshold values presented here will result in the selection of more effective marten and fisher traps and should therefore be incorporated into Canadian standards and considered at the international level.

With the implementation of the marten trap standard proposed here, the Conibear 120, the Sauvageau 2001-5 and all the other traps rating below the kill threshold line should be replaced by the C120 Magnum and Kania traps. Both traps have been manufactured and marketed for at least 5 years.

There are no commercial traps that meet the new proposed standard for the effective harvest of fishers. Despite the fact that the Bionic has been known to be an effective trap for many years (Proulx and Barrett 1993a) and that it was even redesigned to simplify its manufacture and improve its longevity (Proulx 1991), this trap is still unavailable on the market. In the absence of acceptable killing devices, box traps are therefore the only traps that can presently ensure the effective capture of fishers (Proulx and Barrett 1994).

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DETECTION SURVEYS FOR FISHERS AND AMERICAN MARTENS IN CALIFORNIA, 1989-1994: SUMMARY AND INTERPRETATIONS

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Abstract: Commercial trapping of fishers (*Martes pennanti*) and American martens (*M. americana*) has been prohibited in California since the mid-1900's, yet concern continues to exist about the status of their populations. Recently developed methods for detecting the presence of forest carnivores have made it possible to estimate their distributions and, potentially, to index their populations. We summarize the characteristics and results of track-plate and line-triggered camera surveys that were conducted in California to determine the presence of fishers or martens in areas scheduled for timber harvest or recreational development. Our objectives were to examine the relationship of survey characteristics to survey success and to compile information that can be used to improve detection methods and refine proposals for monitoring population abundance. Secondarily, we mapped the survey locations and results to help describe the current distribution of *Martes* in California. A total of 225 surveys averaged 18.3 stations and 12.6 days per

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survey. About 40% of the surveys detected at least one of the species; 3.6% detected both. Fishers were detected after an average latency of 3.4 days; martens, after 3.3 days. Multivariate regression indicated that success at detecting fishers may be affected more by survey duration than by survey extent. Surveys that were successful at detecting either fishers or martens had significantly greater effort (number of stations × duration) than surveys that were unsuccessful. Martens appear well-distributed in the Sierra Nevada/Southern Cascades but were not detected in the Coast Range or Klamath Mountains. Fishers were commonly detected in northwestern California but in the Sierra Nevada were not detected north of Yosemite National Park. The high proportion of successful surveys, the low latencies to first detection, the fact that both methods produced independently verifiable results, and their low cost make track plates and line-triggered cameras effective means for detecting martens and fishers and describing their distributions.

Introduction

Commercial trapping of fishers (*Martes pennanti*) and American martens (*M. americana*) in California was suspended in 1946 and 1954, respectively, due to a perception that the combination of trapping mortality and habitat loss by logging was leading to the decline of both species (Dixon 1925, Grinnell et al. 1937). Concern about the status of fisher and marten in California has increased despite the protection of these species from trapping (Schempf and White 1977, Buskirk and Ruggiero 1994, Powell and Zielinski 1994, Gibilisco 1994). The cessation of trapping was coincident with a period when timber harvest and human population in California dramatically increased (Forest and Rangeland Resources Assessment Program 1988, McKelvey and Johnston 1992).

Suspicions that habitat loss would negatively affect fisher and marten populations and a perceived decline in the number of sightings in California prompted a variety of conservation actions in the 1980s and 1990s. Most fisher and marten habitat in California occurs on land managed by the US Department of Agriculture Forest Service, and under the provisions of the National Forest Management Act (NFMA) the fishers and martens in California have been designated as species "sensitive" to forest management activities. This designation entitles them to "special management emphasis to ensure their viability and to preclude trends toward endangerment that would result in the need for Federal listing [under the Endangered Species Act (ESA)]" (Forest Service Manual 2670.32). The public have registered their concern directly by submitting 2 petitions (in 5 years) to list the fisher in the western United States under the federal Endangered Species Act (Central Sierra Nevada Audubon Society et al. 1990, Biodiversity Legal Foundation 1994).

With the cessation of trapping in the mid-1900s a source of verifiable data on the status and distribution of *Martes* in California was lost. Until recently, the haphazard accumulation of sightings of each species and interviews of resource

managers has been the sum total of effort to monitor their status since the seasons closed. This information has periodically been summarized for all or parts of the state (Schempf and White 1977; E. Burkett, California Fish and Game, pers. commun. 1992; Gibilisco 1994) but unknown qualifications of the observers, the similarity of appearance of fishers and martens, and the lack of a standardized approach affect the reliability of these reviews.

It has become clear that a random collection of sightings of dubious accuracy is not appropriate to fulfill the mandates of NFMA, to acquire the information necessary to justify listing under ESA, or to base responsible forest management. This data vacuum prompted the development of standardized detection methodology for fishers and martens in proposed management activity areas in California (Zielinski 1991). The present paper summarizes the results of 225 surveys that used the 2 primary methods of detection during the period 1989-1994: enclosed track plates and line-triggered 110 cameras (Barrett 1983, Jones and Raphael 1993, Fowler and Golightly 1994, Zielinski and Kucera 1995a).

Our objectives were to (1) summarize the effort expended during the period 1989-1994, (2) describe the results in terms of survey methodology and survey success, (3) help describe the current distribution of both species in California, and (4) compile information that can be used to improve detection methods and refine proposals for monitoring population abundance (e.g., Zielinski and Stauffer 1996). It is important to know the minimum amount of effort, in days and in number of stations, necessary to ensure a reasonable chance of detecting a target species if it is present. We investigated those variables which affect survey success, and we also focused on how long it takes to detect a target species (latency to first detection). This information can be used to improve the protocols used in more rigorous, planned, and comprehensive attempts to detect target individuals and to monitor populations. Although the data were collected in California the methods used and conclusions drawn should be applicable to other areas where the conservation of *Martes* species is a concern.

Methods

Field

In 1991 a survey protocol was distributed to biologists in each district of each national forest in California and to other biologists interested in determining whether fishers or martens occur in areas proposed for timber harvest or recreational development (Zielinski 1991). This methodology was adapted from a number of ongoing efforts to refine survey techniques for forest carnivores (Barrett 1983, Jones and Raphael 1993, Fowler and Golightly 1994).

Each survey included multiple-detection stations that were distributed at 0.8 km intervals along roads throughout the project area and a 0.8 km buffer around

it. Most surveys were conducted in roaded areas, but in roadless areas (>2.4 km from a road) a similar array was used. Each station consisted of a rectangular plywood box that enclosed an aluminum plate sooted with either acetylene or kerosene. A piece of chicken was placed at the rear of the plate and the distal third of the plate was covered with white Con-Tact™ paper. Animals attracted to the bait enter the box, tread on the soot, and leave footprints on the white paper. Most stations were checked every 2 days for a minimum of 12 days. At each visit the plate was checked for tracks, bait was replaced and, if necessary, a new plate was installed. Most biologists planning a survey submitted a short survey plan to our laboratory prior to field work that included a brief description of the survey area and a map identifying the proposed station locations.

The majority of surveys were conducted by Forest Service biologists, and in a manner consistent with the intent of the protocol. Surveys were required to have *at least* 4 detection devices (track plates or line-triggered cameras), spaced about 0.8 km apart and checked for a minimum of 6 days to be included in our summary. Surveys meeting these criteria and that were conducted between July 1989 and December 1994 were eligible for inclusion. Surveys conducted as precursors to research studies were usually more extensive than the typical project-area survey and some surveys, particularly a few conducted by consultants on private land, were less rigorous than desired but the few surveys of this nature were also included.

The survey location and timing were beyond our control because they were dictated by local management activities, availability of funds, and the schedules of local biologists and of volunteers that sometimes helped the biologists. Therefore, the dispersion of surveys across space, among forest types, and across elevations was uncontrolled. A survey was considered distinct when it occurred at a unique time and place. When surveys were run more than once at the same location only the first survey was included in our summary. Adjacent surveys conducted at least 4 weeks apart were considered distinct, but certainly not independent because the same animal (particularly fishers with their larger home ranges) could be detected during each survey. However, surveys that were adjacent *and* sequential were uncommon. If 2 survey areas were within 1.6 km and were run simultaneously, they were pooled and considered a single survey. Most surveys were conducted in either early spring or late fall. Winter surveys were discouraged because snow interfered with the schedule to check the stations and could also affect the mobility of fishers and martens and their ability to find the stations.

Habitat data were not always collected at each station location and the data that are available are visual assessments collected by dozens of different observers. We have not analyzed these data. However, we assume that the biologist planning the survey was familiar with the geographic distribution and general habitat associations of the target species. This assumption was validated for many of the surveys when the survey plans were reviewed. During this review, we realized

that biologists more often conducted surveys at elevations and in forest types where fisher, rather than marten, were likely to occur. This result probably occurred because of the widespread understanding that the status of fishers was more uncertain than that of martens.

When our work began, there was no quantitative method to distinguish the tracks of fishers and martens (Taylor and Raphael 1988) so the protocol recommended that when a possible fisher or marten track was discovered that a secondary device, the line-triggered camera (Jones and Raphael 1993), immediately be established at the site to verify the identity of the species. Shortly thereafter a discriminant function was developed that could distinguish the tracks of both species (Zielinski and Truex 1995). In 1993, when the preliminary results of this work were known, the use of line-triggered cameras at the location of a track-plate detection was discontinued.

Although track-plates were the primary detection device in the majority of surveys, some surveys were conducted by biologists who favored the line-triggered camera as the primary detection device, especially before the protocol was released. When line-triggered cameras were the only device used in the survey, they were deployed and checked in the same fashion as the track-plate boxes.

Laboratory

A database was established using Oracle software (version 6.0, Oracle Corporation, Belmont, California) to manage the survey results. Information about the proposed survey date, location, and survey characteristics (e.g. proposed duration, check interval, number of stations, primary detection device) was entered when the survey plan was received, and corrected if necessary, and completed when the survey results were submitted. Surveyors were instructed to remove the Con-Tact paper from plates that had tracks that resembled those of either fisher or marten and to protect them in an acetate document folder. The identity of all tracks and photographs was verified by the authors (WJZ or RLT); if surveyors did not submit either a track or photograph the survey was considered unsuccessful. Questionable tracks were measured and identified according to the methods outlined in Zielinski and Truex (1995).

The location of the center of each survey was visually estimated from a survey map and the UTM (Universal Transverse Mercator) coordinates for all surveys were used to create a map in a Geographic Information System (GIS) (ARC/INFO 6.1.2). The GIS also included a dominant vegetation type layer, commonly referred to as CALVEG (Matyas and Parker 1980) that was derived by visual interpretation of color infra-red satellite imagery. Polygons mapped at 1:250,000 and classified as 1 of 300 vegetation series were aggregated into 42 unit types at a scale of 1:1,000,000. CALVEG identifies only the existing vegetation type and does not include information about the developmental condition of the vegetation in the polygons.

Data were output to SAS (SAS Institute Inc., Cary, North Carolina) for analysis. Using *t*-tests and regression methods, we explored the factors that affect 2 primary response variables: latency to first detection (in days; LFD) and proportion of surveys that were successful. Independent variables included survey duration, number of stations in the survey, and effort (number of stations × duration of survey).

Results

Survey Characteristics

In total, 225 surveys were used in our analysis, representing 4847 survey days and 3799 stations checked 1377 times. Because data were missing for some variables, not all data were used for each analysis. For example, not all surveys reported the latency to first detection. Surveys were conducted in 17 counties and 11 national forests in California. Track plates were the primary device for 180 surveys that had sufficient data for analysis of survey success; line-triggered cameras were the primary device for 21 surveys. Surveys averaged (± SD) 18.3 ± 13.2 stations and were run an average of 12.6 ± 3.9 days each. In about 80% of the surveys, the stations were checked for visits by a fisher or a marten every 2 days. Effort varied considerably, from 24 to over 4000 station-days (station-day = 1 station checked 1 day = 1 unit of effort) (Fig. 1).

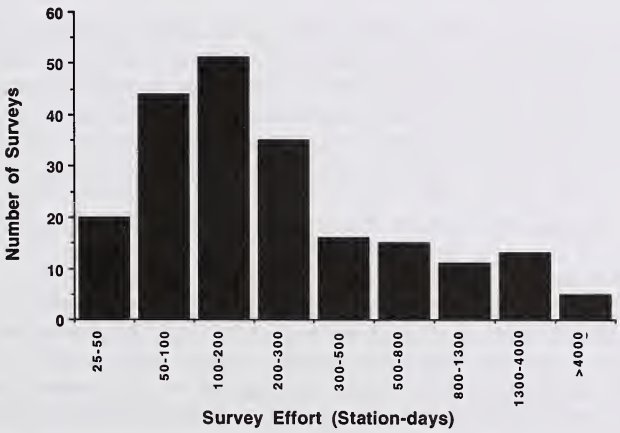

Figure 1. Frequency distribution of survey effort (number of stations × number of survey days) for 221 surveys conducted in California from 1989-1994.

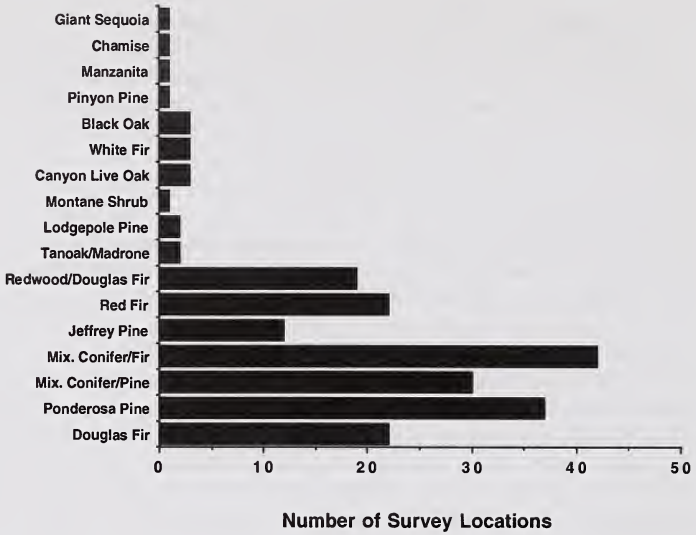

Figure 2. Frequency distribution of CALVEG (Matyas and Parker 1980) vegetation types where surveys occurred.

Most surveys occurred in mixed conifer and ponderosa pine (*Pinus ponderosa*) CALVEG types, with Douglas-fir (*Pseudotsuga menziesii*), redwood (*Sequoia sempervirens*)/Douglas-fir, and red fir (*Abies magnifica*) types also common (Fig. 2). Three latitudinal zones, about 2° 15' each, were created to describe the elevational distribution of surveys. Surveys in the north occurred at a mean elevation of 1137 ± 583 m, at 1792 ± 463 m in the central region, and at 2017 ± 317 m in the south (Fig. 3), which reflects the inverse relationship between latitude and elevation on the distribution of *Martes* habitat.

Survey Results

Eighty-nine (40.3%) of the 221 surveys had at least 1 station that detected either marten or fisher; 52 (23.5%) detected fisher, 37 (16.7%) detected marten, and 8 (3.6%) detected both. A total of 814 detections of either species was recorded, including multiple detections per station as well as detections at multiple stations per survey. Fishers were detected at 39 (21.7%) of the track-plate surveys and 11 (52.4%) of the line-triggered camera surveys; martens were detected at 31 (17.2%) and 5 (23.8 %), respectively, of these surveys.

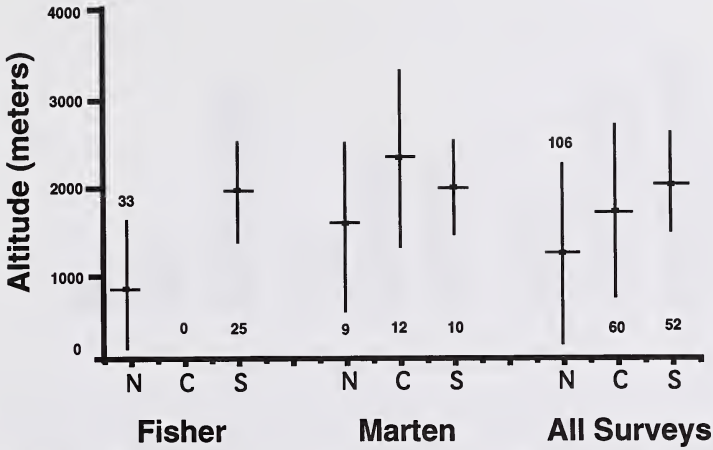

Figure 3. Elevational distribution of 218 surveys, surveys where fishers were detected (n = 58), and surveys where martens were detected (n = 31). N, C, and S represent Northern, Central and Southern latitudinal zones, separated by about 2 degrees and 10 minutes latitude each. Horizontal bars are means and vertical bars are 95% confidence intervals. The numbers above or below each bar are the sample sizes.

Survey Success, Number of Stations, and Effort: Surveys with 4-8 stations had less than half the success rate at detecting either species compared with those surveys with at least 20 stations (Fig. 4), but these differences were not statistically significant. Surveys that succeeded in detecting either species involved expending significantly more effort than surveys that did not (t-test, $P < 0.05$), a phenomenon that occurred even when the number of stations was as few as 6-10 (Fig. 5).

Latency to First and Second Detection: Fishers were first detected after a mean of 3.4 days; martens, after a mean of 3.3 days (Table 1). Each species was detected before about 30% of the total survey duration had elapsed, regardless of the number of stations in the survey (Table 2). Twenty-one surveys detected either fisher or marten more than once, and at a different station than where the first detection occurred. This second detection occurred an average of 6.7 days after the survey began for fishers, and 3.9 days for martens (Table 1). Martens were detected at a second station in a survey significantly sooner than were fishers (t = 2.66, df = 20, P = 0.01).

Table 1. Mean (± SD) latencies to first and second detection (days) for surveys that detected fishers or martens using either track plates or line-triggered cameras. All surveys had at least 4 stations and were checked every 2-3 days.

	No. Surveys	No. Surveys With Detections	Latency (in days)	
			First Detection	Second Detection
Fishers:				
All surveys	169	39	3.41 ± 2.06	6.72 ± 4.23
Track plate only	151	32	3.37 ± 1.93	-
Line-triggered camera only	18	7	3.86 ± 2.67	-
Martens:				
All Surveys	169	21	3.33 ± 2.58	3.94 ± 2.25
Track plate only	151	18	3.39 ± 2.64	-
Line-triggered camera only	18	3	4.33 ± 2.89	-

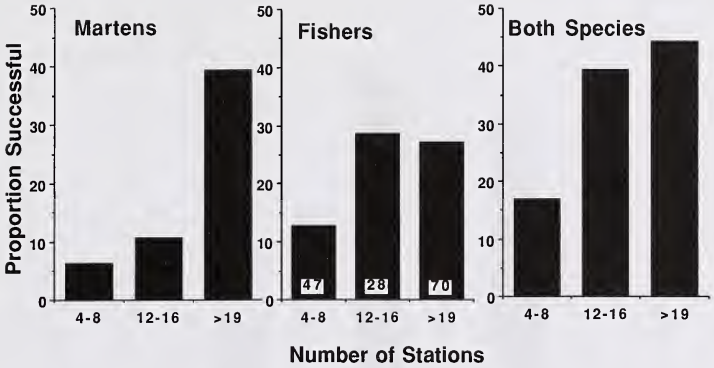

Figure 4. Proportion of surveys (%) that were successful at detecting martens, fishers and either species as a function of the number of stations in the survey. Numbers at the base of bars in the fisher panel are the sample sizes for the station groupings for all panels.

LFD and Type of Detection Device: Surveys that used only track plates detected fishers and martens after a mean of 3.2 and 2.4 days, respectively, whereas surveys that used only line-triggered cameras did so after 3.9 and 4.3 days (Table 1). In those surveys where line-triggered cameras were used to verify the identity of the species detected at a track plate (n = 56), fishers returned to be photographed at the same station on 12 occasions, after a mean of 5.9 days, and martens returned and were photographed on 9 occasions, after a mean of 3.3 days.

Table 2. Ratios (± SD) of latency to first detection/survey duration (both in days) for surveys with different numbers of stations.

Number of Stations	Fisher	Marten
>3	0.27 ± 0.2	0.30 ± 0.2
>9	0.27 ± 0.2	0.28 ± 0.2
>19	0.22 ± 0.1	0.25 ± 0.2
6-10[a]	0.32 ± 0.2	0.34 ± 0.2

[a] This grouping included because it is the number of stations per sampling unit in the monitoring program proposed by Zielinski and Stauffer (1996).

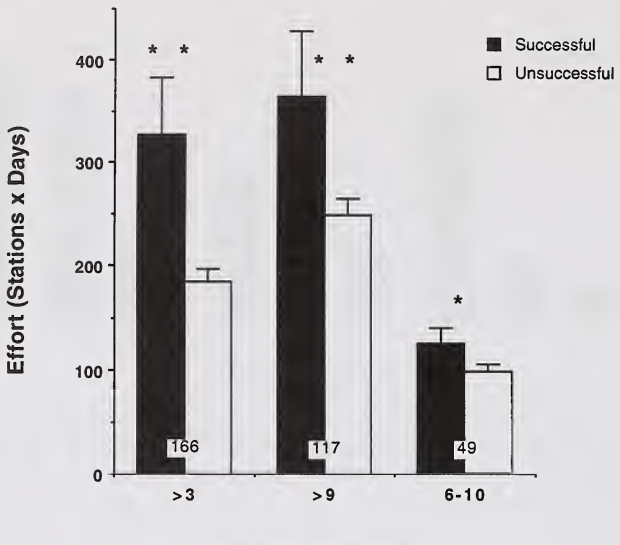

Figure 5. Amount of effort (number of stations × the number of days) expended for surveys that were successful (solid bars) or unsuccessful (open bars) for 3 station-number groupings. The 6-10 grouping was chosen because it is the number of stations per sampling unit in the monitoring program proposed by Zielinski and Stauffer (1996). Asterisks indicate significant differences in *t*-tests ($P < 0.05$) and numbers at the base of the bars are sample sizes.

LFD, Number of Stations, Survey Duration, and Effort: There was no relationship between the number of stations in the survey and the LFD ($r^2 = 0.083$, $P > 0.05$), though there was a suggestion that as number of stations increased the latency decreased (Fig. 6). There was also no linear relationship between LFD and survey duration ($r^2 = 0.489$, df = 79, $P > 0.05$) nor a relationship between LFD and effort ($r^2 = 0.008$, df = 79, $P > 0.05$). However, when the number of stations in the survey, the duration of the survey, the survey area, and survey effort were included in a multiple regression, the full model was significant, but only for fisher, and the duration of the survey and effort were the 2 variables most responsible for the relationship (Table 3).

Geographic Distributions: Fishers were primarily detected in 2 areas of the state: the northern Coast Ranges/Klamath Mountains and the southern Sierra Nevada (Fig. 7A, B). Fishers were not detected in the southern Cascades or

Table 3. Multiple regression, with stepwise selection, relating the number of stations in the survey, number of days in the survey, effort, and survey area to the LFD for fishers and martens.

Source	df	Mean Square	F	Prob > F	Variable	Prob > t
Fishers:						
Model	4	10.69	3.023	0.031	Effort	0.008
Error	33	3.53			Number of Days	0.009
					Survey Area	0.182
					Number of Stations	0.209
Martens:						
Model	4	1.67	0.204	0.9323	Effort	0.692
Error	16	8.16			Number of Days	0.876
					Survey Area	0.817
					Number of Stations	0.638

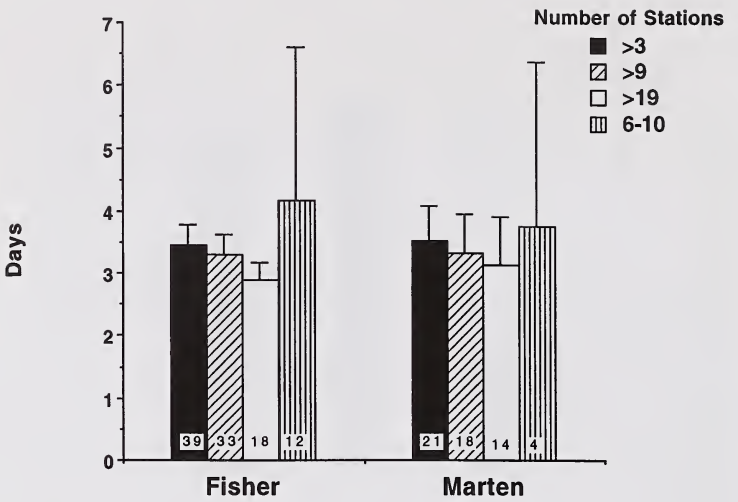

Figure 6. Mean (± SE) latency to first detection (in days) as a function of the number of stations in the survey. The 6-10 grouping was chosen because it is the number of stations per sampling unit in the monitoring program proposed by Zielinski and Stauffer (1996). Sample sizes are presented at the base of each bar.

northern and central Sierra Nevada, an area where they historically occurred (Grinnell et al. 1937). Martens were not detected in the northern Coast Ranges and Klamath Mountains, which includes the entire range of *M. a. humboldtensis* (Fig. 8A). However, martens are well distributed in the southern Cascades and Sierra Nevada (Fig. 8B). Both species were detected together only in the southern Sierra Nevada, where in a few instances an individual of each species visited the same track plate or camera station. Significant areas of the ranges of each species received little survey effort in this retrospective analysis, including several counties in the northern Sierra Nevada, the southern part of the northern Coast Ranges, and the upper elevations of the Klamath Mountains.

Discussion

Track plates and line-triggered cameras are efficient means for detecting the presence of fishers and martens. Twenty-three percent of the surveys detected fishers and 16% detected martens, even when the location of surveys was not

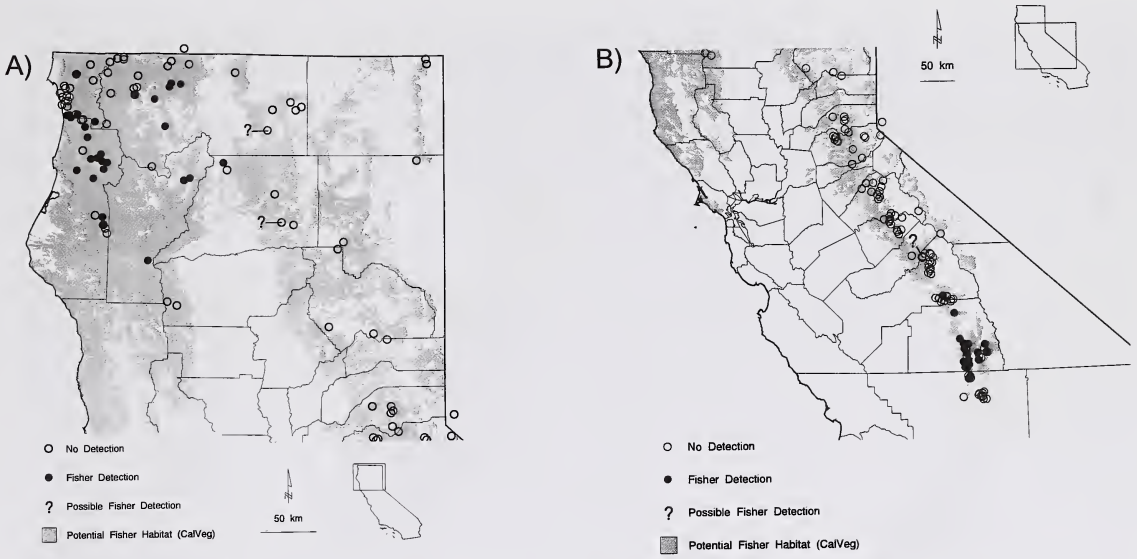

Figure 7. A. Northern California, and B. Central California, distributions of surveys that detected fishers (solid circles) and those that did not (open circles). Question marks denote surveys where a fisher track was reported but was either not submitted for verification or was of marginal quality for verification. Gray background is the distribution of CALVEG (Matyas and Parker 1980) vegetation types considered suitable fisher habitat. This included: Douglas fir-tanoak-madrone, Douglas fir-pine-madrone, Jeffrey pine, tanoak-madrone, madrone-black oak, mixed conifer-fir, mixed conifer-pine, Oregon white oak, ponderosa pine, redwood-Douglas fir, white fir.

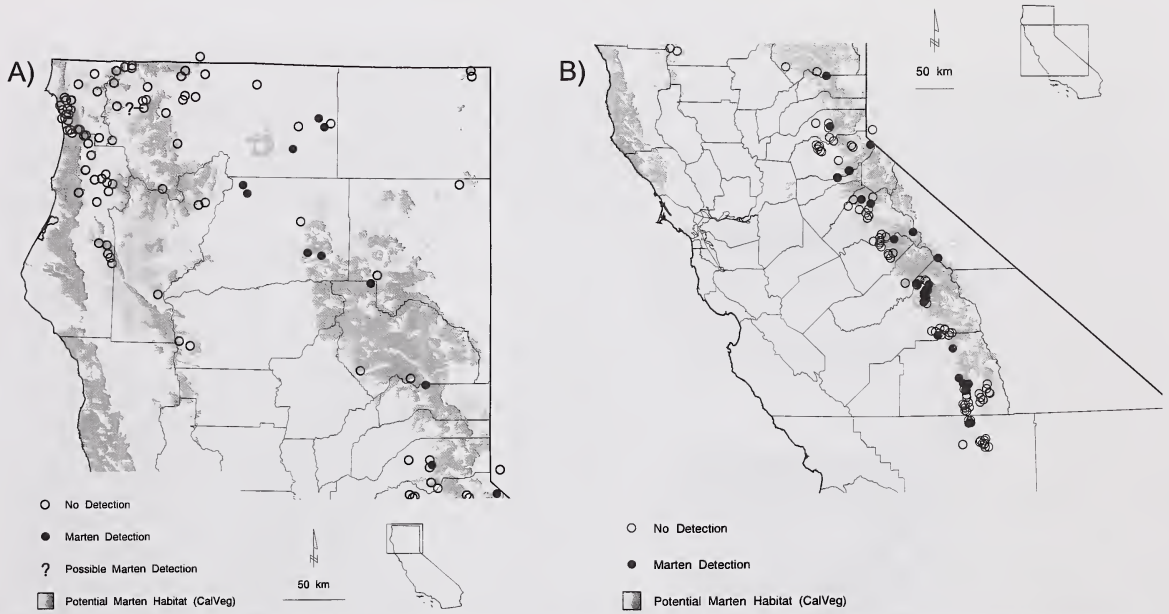

Figure 8. A. Northern California, and B. Central California, distributions of surveys that detected martens (solid circles) and those that did not (open circles). Question marks denote surveys where a marten track was reported but was either not submitted for verification or was of marginal quality for verification. Gray background is the distribution of CALVEG (Matyas and Parker 1980) vegetation types considered suitable marten habitat. This included: red fir, white fir, mountain hemlock, redwood-Douglas fir, lodgepole pine, mixed conifer-fir, Douglas fir-tanoak-madrone, Douglas fir-pine-madrone, Jeffrey pine.

controlled and some surveys were undoubtedly in inappropriate habitat. Another measure of their utility is the short duration, 3-4 days, before 1 or the other species was verified in a survey area. In addition to determining occurrence, these methods were also useful for describing the current distributions at state and regional scales. Collectively, these surveys provided a more reliable understanding of a species' range than does a summary of incidental sightings of unknown accuracy because each record can be independently verified. Although sighting data can be screened for reliability (e.g., Aubry and Houston 1992), and perhaps can be gathered more economically than conducting field detection surveys, we believe that sighting data should be used to augment, not substitute for, surveys using track plates or cameras.

Although the inferences we can draw from the present summaries are limited by the number of uncontrolled variables, a number of interpretations can be made that will benefit future monitoring and detection efforts. That fishers and martens were detected after a mean of only 3 or 4 days reinforces the conclusion that a maximum survey period of about 2 weeks is probably sufficient, provided a reasonable number of stations are used and distributed as recommended. Even the upper confidence limits on LFD, 7.5 days for fishers and 8.4 days for martens, occurred before the end of the recommended duration. A series of surveys (n = 48) of 22 days each were recently completed on commercial forest land in northwestern California (R. Klug, Simpson Timber Co., pers. commun. 1995) and the mean LFD for fishers (martens do not occur in the study area) was about 12 days (n = 31), or 3 times the LFD reported here. However, each survey had only 6 stations, which may have influenced LFD. This result may also have been specific to the relatively small area sampled (and consequently fewer individuals included) compared to the summary of statewide surveys reported here. Regardless of the length of survey or the number of stations in the survey, the first detections in our data set almost always occurred before 30% of the intended survey duration had elapsed and the second detection (at a different station) occurred shortly thereafter.

Some of the most important methodological questions, namely how many stations are required and how long they should be run to achieve a particular probability of detection, are difficult to answer using the type of data summarized here. Sampling rigor was unregulated, and sampling locations and timing were determined by management needs, motivation of local biologists, and the availability of funds and personnel. It was perhaps this lack of strict control on methods and sampling design that made it difficult to elucidate factors that affect survey success. For example, it is logical to assume that as the number of stations in the survey increases, the time until 1 of them is visited by a target species should decrease. Although our analysis did not confirm this prediction, the trend was in the correct direction. The failure to find a statistically significant relationship

between these variables may have been due, in part, to a lack of control of habitat and landscape suitability. The CALVEG data suggest that a number of surveys were conducted in general vegetation types that were not considered suitable by our standards, and it is possible that surveys were not conducted in the most suitable seral stages of otherwise suitable vegetation types. Furthermore, we did not assess landscape effects on habitat suitability (e.g., Rosenberg and Raphael 1986).

The data for fisher detections suggest that the number of stations in a survey may be less important than the duration of the survey. Although station number and survey duration certainly combine to affect survey success, determining the minimum number of stations to use given a specific survey duration is difficult. Surveys that had as few as 6-10 stations were still successful if they expended about 120 units of effort or more (Fig. 5). Using 8 stations this is accomplished with a survey lasting at least 15 days. Although a greater number of stations should probably be used, simply because the detection of rare carnivores dictates that effort be as liberal as can be afforded, it seems that surveys with as few as 6-10 stations can be as successful as those with more stations provided the stations are in place for at least 2 weeks. However, we caution that our retrospective analyses are not well suited to drawing strong inferences.

The ideal way to evaluate methods would be to control for the presence and abundance of the target species. In no case was the presence of fishers or martens verified before the surveys summarized here were conducted. However, our summary compensates for lack of experimental rigor with sample size. It would be very difficult to conduct a single research study that included 225 surveys (and almost 4000 stations) across the state of California, especially if it was necessary to precede each survey with a mark-recapture or radio-telemetry effort so that the occurrence of the target species at each location was known. A practical compromise might be to at least stratify the sampling area by habitat type and seral stage (using a more comprehensive dataset than CALVEG) prior to conducting the surveys. This approach is proposed by Zielinski and Stauffer (1996) in a population monitoring scheme that determines the sampling effort to detect declines in an index of abundance of fishers or martens in California.

The distribution of successful and unsuccessful surveys is an important assessment of the current status of both species in California. This paper is not intended to be a description of the current distributions because it reviews only 2 methods used to verify presence. However, our data comprise the bulk of the data used recently to create range maps (Kucera et al. 1995; Zielinski et al. 1995). Fishers appear to be very uncommon in the southern Cascades and throughout much of the Sierra Nevada. Although some very recent photographs of a fisher at a camera station (L. Chow, National Biological Service, pers. commun. 1995) and several roadkills suggest the presence of the species just north of the sub-

population depicted in the extreme southern Sierra Nevada in Figure 7B, the detections occurred after considerable previous survey effort. A few recent sightings of fishers have been reported in the northern Sierra Nevada (E. Burkett, California Fish and Game, pers. commun. 1995) but mistaking other species for fishers, especially the more abundant marten, is common (W. Zielinski, pers. obs.; R. Golightly, Humboldt State University, pers. commun. 1994).

The distribution of martens also appears to have changed since it was first described (Grinnell et al. 1937). Surveys indicate that martens are well distributed throughout the Sierra Nevada and Cascades in California, but the absence of marten detections in the range of *M. a. humboldtensis* is of concern. Although surveys were not common at the higher elevations in the Klamath Mountains, which appear to include some typical marten habitat, the absence of any marten detections in the redwood and Douglas-fir types in this region indicates that if the Humboldt marten still exists it does so at very low densities. Surveys were recently conducted in the redwood type along the coastline in northwestern California (R. Klug, Simpson Timber Co., pers. commun. 1994; R. Golightly, Humboldt State University, pers. commun. 1994). No martens were detected, and with the exception of several fisher detections near the coast the results do not substantially alter the distributions presented here.

Both track-plate and line-triggered camera stations were effective at detecting martens and fishers, but both species were detected in a higher percentage of surveys that used only line-trigger cameras than surveys that used only track plates (fishers: 52.4% *versus* 21.7%; martens: 23.8% *versus* 17.2%). Much of this difference is probably accounted for by the fact that camera-only surveys occurred most frequently in the extreme southern Sierra Nevada where both species are relatively common and frequently sympatric. Previous work suggests that cameras are somewhat less effective at detecting martens than track plates (Bull et al. 1992, Fowler and Golightly 1994). Had surveys using the 2 devices been conducted with control for geographic location, it is likely that the results would have been similar. However, line-triggered cameras have the disadvantage of being more fragile and prone to malfunction than track-plate stations and being incapable of detecting a second visit to the station between rebaiting (Zielinski and Kucera 1995b).

Surveys that use single-sensor 35-mm cameras (Kucera and Barrett 1993, Kucera et al. 1995) were uncommon during the period summarized here, largely because their significant cost limits the number that can be deployed. The results from 35-mm cameras were excluded from this summary because of the infrequent use of these cameras and absence of a standard protocol during the assessment period. However, more detailed maps of the distributions of martens and fishers have recently been published that were created from the combined results of 35-mm cameras, line-triggered cameras, track plates and other miscellaneous verifiable records (Kucera et al. 1995; Zielinski et al. 1995).

The knowledge that most surveys that include 6-10 stations and are run for at least 12 days will detect either a marten or fisher, if present, in less than 4 days provides a strong foundation for new detection protocols and for sampling designs that monitor changes in abundance and distribution. These results have already been influential in proposals for a new detection protocol that will be applied throughout the western U.S. (Zielinski and Kucera 1995a) and a scheme for monitoring changes in an index of fisher and marten abundance in California (Zielinski and Stauffer 1996). Current survey methods are quite good at documenting that either fishers or martens are present in an area. However, we are much less confident in declaring a species absent when it is not detected. Careful quantification of future detection and monitoring efforts, combined with more experimental work in areas where presence and abundance of target species has been confirmed, will improve our confidence in establishing presence and absence.

Acknowledgments

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Part V

Martes Management

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SOCIO-ECONOMIC ASPECTS OF MARTEN MANAGEMENT

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Abstract: Traditionally, species like the American marten (*Martes americana*) were managed on the basis of their contribution to well-defined market uses. These market values provided evidence of the value of the species, in a limited sense. These values, however, are often in conflict with other land uses, particularly extractive activities like forestry, oil and gas exploration and mining, as well as conversions of forest habitat to other land uses. The market value component of species like marten reflects only a small portion of their social value since these species are also valued for their contribution to ecosystems and their role in enhancing recreational experiences. However, non-market values are difficult to measure and are difficult to incorporate into management and planning. In this paper the issues surrounding the economics of species like the American marten are discussed. A case study of the benefits and costs of marten management in Newfoundland is used to illustrate the approaches currently being used to examine the socio-economic aspects of marten management. This case study also illustrates some of the challenges involved in making trade-offs regarding conservation decisions.

Introduction

Traditionally, species like the American marten (*Martes americana*) were managed on the basis of their contribution to well-defined market uses, such as the fur trade. These market values provided evidence of the value of the species, in a limited sense. These values, however, are often in conflict with other land uses, particularly extractive activities like forestry, oil and gas exploration and mining, as well as conversions of forest habitat to other land uses. When such conflicts arise, the higher valued use typically wins out. Consideration for marten habitat is undermined.

The market value component of species like marten, however, reflects only a small portion of their social value since these species are also valued for their contribution to ecosystems and their role in enhancing recreational experiences.

However, these "non-market" values are difficult to measure and are difficult to incorporate into management and planning. In this paper the issues surrounding the economics of species like the American marten are discussed. After an overview of the traditional economic base of marten harvesting, the issue of non-market values associated with marten is presented. This "new" approach to the economic analysis of species like marten is employed in an analysis of American marten conservation in Newfoundland. A heuristic benefit-cost analysis of an American marten conservation program was performed. The paper concludes with an investigation of the problematic issues surrounding this type of analysis and a discussion of topics for further research.

The Economics of Marten - Basic Analytics

Traditionally, economic aspects of species like marten have been examined using their value as fur. Figure 1 provides the values of marten harvests and harvest levels over the time period 1970-1993. Note that the average value per unit ranged from about $25 to about $100 in real 1986 Canadian dollars. Values of harvests have fallen over the past few years to just under $5M.

In order to put these numbers into perspective, it is instructive to consider competing demands on the land base, namely, forestry and energy extraction uses of the land. Using aggregate values for a portion of the boreal forest in Alberta, we constructed the following values. One square kilometre of forest land provides an annual revenue of between $4500 and $7500 (1995 dollars, depending on the assumed price per cubic metre of wood). Given these values it would take less than 1200 km^2 of productive forest land to yield more revenue than

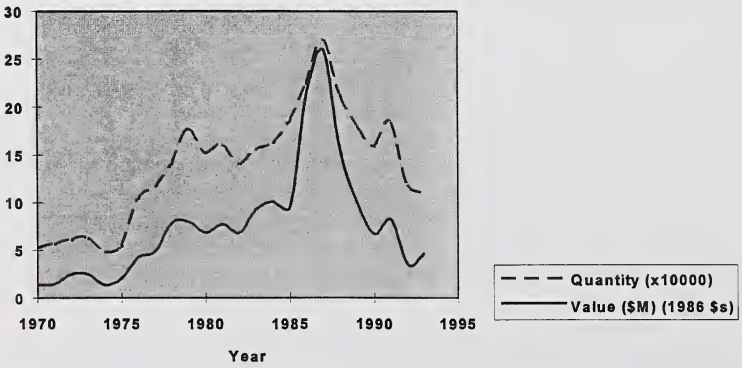

Figure 1. Marten harvest statistics. (Source: CANSIM database, various years.)

the nation's entire current revenue from marten harvest. If we examine energy resource royalties on this basis, 1 km^2 of productive oil and gas area yields approximately $4,000 in royalties (not revenues) per year. Thus, it would only take 1500 km^2 of energy-producing land to produce as much in royalties as is currently captured in revenue nationally from marten harvesting. Clearly, when marten habitat concerns are in conflict with forestry or oil/gas resource use concerns, the market-based measures of value favor the latter uses. This bias does not mean that forestry, energy and wildlife land uses are mutually exclusive, nor are they always in conflict. The point is that the economic significance of marten harvest is minimal relative to other land uses and thus scarcity signals that indicate a need for habitat enhancement or species conservation may go unwarranted.

Although marten have low value in terms of fur harvest, this does not mean that the species is economically unimportant. Values like fur harvest are market values since they are expressed in a market. Marten may also contribute to non-market values. Non-market values are categorized as "use" values and "passive use" values. Use values are values that are related to some use, activity or traceable economic behavioral trail. Outdoor recreation typically requires expenditures on travel and other goods and thus even though recreation may not be priced in a market, expenditures on recreation-related items provide a behavioral trail that can be used to develop a value. Effects of changes in scenery or aesthetic attributes of forest environments on real estate values can also be considered use values. In the case of use values, marten may contribute to the enhancement of recreational experiences, or the linkages between marten and other ecosystem components may affect recreational values or other directly measurable economic values.

Passive use values, on the other hand, have no clear behavioral trail. These values include existence values, bequest values and other values that are not typically expressed through any market directly or indirectly. Even though an individual has never seen, and may never see a marten, this individual may be willing to make tradeoffs to ensure that marten will be available for future generations. In the case of the American marten, a threatened species in Newfoundland, individuals may be concerned about the existence of the species, and thus exhibit existence values. Alternately, individuals may recognize value for wilderness areas, which may include species like marten as a significant component.

There has been a considerable amount of debate about passive use values and their measurement. These measures are challenging to determine and use in economic analysis. Nevertheless, they may form an important component of the economic aspects of species like marten (see Smith 1990 for a review of environmental valuation issues). In the remainder of the paper, we focus on an analysis of the non-market benefits of the American marten in Newfoundland. We consider the case of an American marten conservation area and use economic

analysis tools to assess such a program. In this case we focus on the tradeoff between forestry activity and passive use values associated with the American marten.

Passive Use Values

Passive use value is defined as individual willingness to pay for an environmental good, even though the individual may never intend to make any active use of it. The individuals derive satisfaction from the mere existence of the good. Since there is no behavioral trail, only direct survey methods can be used to elicit passive use values. The most popular of these methods is the contingent valuation method (see Adamowicz [1991, 1992] for a review of non-market valuation methods). This technique constructs a situation in which a hypothetical market is constructed and individuals vote on whether or not they would accept additional tax payments (for example) in exchange for increased provision of an environmental good (Mitchell and Carson 1989).

It is worth noting that there is still considerable controversy about the existence of passive use values (not just their measurement) and whether passive use values are an economic phenomenon (Hausman 1993, Hanemann 1994). Passive use values (assuming they exist and are relevant) are associated with public goods or quasi public goods. A public good is one which no one can be excluded from and no one person's consumption reduces another's. Wilderness areas, wildlife habitat, protected areas and other such environmental goods are examples of public goods. However, because no one can be excluded from the benefits of such goods, there is a tendency to underprovide these goods. Their values are underrepresented because individuals can still enjoy the benefits without incurring any of the costs of provision. Decisions about the production of public goods are clearly collective decisions, and are therefore often very complex, political and economic issues.

Measurement of Passive Use Values Using Contingent Valuation

The forest is a source of multiple outputs or products, including timber, recreation, water and aesthetics. Forests may also generate passive use values; in other words, their existence is an output. A general economic approach to forest management would be to evaluate the outputs, such as timber and non-timber elements, and search for the highest valued uses (either single uses or combinations). It is relatively easy to gather values for timber outputs. However, estimates of passive use values are very rare. Conceptually, however, these values should be included in the economic calculus. In fact, passive use values may be considerably larger than all other values for some ecosystems (where timber

and non-timber use values are low). The measurement of these values, however, has been a contentious issue.

In 1989 the Exxon Valdez crashed and the ensuing oil spill generated a variety of damage assessment cases and calls for compensation (Duffield 1995). One element of compensation demanded by the State of Alaska was lost passive use value. A vigorous debate began in the economics profession that pitted Nobel prize winners against each other, contesting the merits of contingent valuation (CV) as a tool to measure passive use values. Issues of the hypothetical nature of the questions, the lack of information and understanding by respondents, and the potential for strategic behavior were examined and assessed. The result of several years of panels, debates and papers (including a book on the topic sponsored by Exxon) was that the National Oceanic and Atmospheric Administration (NOAA), the agency responsible for the guidelines for damage assessment under the Oil Pollution Act, approved contingent valuation as a method for determining passive use values and initiating discussion on compensation (Arrow et al. 1993).This acts as a precedent for the use of passive use values in resource management decisions. The NOAA report also provided a set of guidelines for conducting contingent valuation studies, and these guidelines will likely be a focal point for researchers, and those assessing research, in the future. What the NOAA panel did reveal is that contingent valuation is quite sensitive to design and procedure, and thus care must be taken in conducting such studies.

Passive use values will continue to be important elements of resource management. Contingent valuation, as a tool, will also continue to be used. One interesting aspect of modern CV passive use value analysis is that a referendum (voting) format is recommended. Thus, CV is very similar to methods used in public opinion polling, except it is more structured than standard opinion polls. As a result, the link between politics, public preference, public participation and economics is made explicit. Since passive use values are not revealed in an economic market, they are being elicited by means of a political market. In this sense, CV results can be interpreted as forms of "structured public input," something that will also continue to be an element of resource management in the future.

A Case Study - An American Marten Conservation Area in Newfoundland

To illustrate an economic approach to the valuation and conservation of the American marten, we apply the results of a recent contingent valuation survey (Condon and Adamowicz 1995) to a forest resource management issue. American marten used to be found in most forested areas in Newfoundland. Today, however, only a small population remains, existing on the west coast of

Newfoundland. An American marten study area was established in 1973 to prevent trapping and snaring. Timber harvesting is also prevented, however, the area contains relatively accessible mature timber. The timber resources are viewed as potential contributors to the economic well being of the region and province.

To analyze the benefits of American marten habitat preservation *versus* timber production, we construct a benefit-cost analysis of maintaining the timber harvesting restrictions in the American marten study area. This benefit-cost analysis includes the calculation of the benefits of timber production (as the opportunity cost of American marten preservation) and the benefits of American marten preservation. The latter are clearly non-market in nature. Furthermore, the benefits of American marten are almost entirely passive use values, since there is no trapping or snaring and the contribution to the enhancement of recreational experiences must be considered as negligible.

The benefits of maintaining an American marten management area were calculated from a contingent valuation survey conducted in Newfoundland in 1992. Details on the survey can be found in Condon (1993) and Condon and Adamowicz (1995). The structure of the contingent valuation survey was a willingness to construct a public trust fund that would be used to manage the American marten area. Individuals were asked to respond Yes or No (in a voting type scheme) to predefined bid amounts. The responses, analyzed using logistic regression models, show that an individual's probability of saying Yes to the payment of the bid amount depends on the size of the bid amount (negatively related), the individual's education (positively related), and the individual's family size (negatively related). Income was not found to be a significant explanatory parameter for the response, but this result is likely due to the fact that education and income are correlated. The model correctly predicted 75% of the responses (Condon and Adamowicz 1995).

Using the contingent valuation model, the mean and median willingness to pay for the American marten area can be calculated. The mean willingness to pay is $28.38 whereas the median willingness to pay is $4.05 (Condon and Adamowicz 1993). The median represents the size of bid at which 50% of the sample would be willing to say Yes to the payment. The mean is the expected value of the willingness to pay distribution. The fact that the mean is larger than the median suggests that individual valuations are different and there are some individuals with very high willingness to pay values (which suggests that there may be significant equity issues involved in a marten preservation program).

Aggregating these values over Newfoundland residents provides a value of $10,430,757 annually (using the mean) and $1,488,533 using the median. Note that aggregating only over Newfoundland residents is probably an underestimate since the benefits of the preservation area probably accrue outside of Newfoundland. However, since the forest resources are provincially "owned,"

we will concentrate on the benefits accruing to Newfoundland residents, recognizing that this is a conservative estimate.

The opportunity cost of the American marten area is the value of the forestry activity in the region. There are many ways that forest activity values can be measured (Milne 1988). We use two different measures, the Net Social Value method, which calculates the difference in annual value added or generated by the forest industry and gross government expenditure on the industry, and the residual timber value method which estimates the delivered price to mills minus harvesting, transportation costs, profit and risk allowances. The first approach is based on analysis by Milne (1988) and the second is based on a study by Deloitte and Touche (1992).

The American marten study area is approximately 35,000 ha in size and contains about 18,000 ha of productive forest land. The softwood volume in this area is over 2 million m^3 and the estimated harvest is approximately 65,000 m^3 annually. Using the net social value method, Milne (1988) suggests a value of \$20.60/m^3 or an annual value of \$1.3 million. Using the residual harvest method, a value of \$15.52/m^3 is derived suggesting an annual value of the area of just over \$1 million. Based on these estimates of value to the forest industry, and the results of the contingent valuation question, residents of Newfoundland find the benefits of the marten study area to outweigh the benefits of forestry activity. Interestingly, this conclusion is supported using either the median or mean estimates of value, and suggests that if the question of maintaining the study area was structured as a referendum in Newfoundland, the majority of residents would support it. However, the opportunity costs of the forest industry have been calculated based on the direct value to the industry. The issue of secondary benefits, such as employment benefits or spin-offs, has not been discussed.

In economic analysis, the topic of secondary benefits has always been a controversial one. The accepted principle is that employment benefits or multiplier effects (spin-offs) are only included as "benefits" if there is chronic or structural unemployment in the economy. The rationale for this principle is that in an economy with near full employment, any employment effects or spin-off effects are transfers from one sector in the economy to another. Jobs created in the forest industry are transfers from other sectors, and they may even create "pecuniary externalities" in that wages in all sectors will be increased, increasing costs to all industries.

In the economy of Newfoundland, however, the assumption of near full employment is probably less reasonable. Thus one could consider employment effects as being at least partly relevant. However, to what degree direct and indirect employment effects are relevant is an open question. One quickly enters into the issue of whether other industries (or other employment opportunities within or outside of Newfoundland) will arise and whether one should consider the

provincial economy as separate from the national economy. Traditionally, economists have downplayed the role of these spin-offs, for good reason, since they tend to overstate the benefits associated with industrial development.

Nevertheless, it is interesting to assess the employment effects associated with the American marten study area. It is estimated that the area would support 120 direct jobs per year. These direct jobs would result in benefits of approximately $4 million to the Newfoundland economy. Incorporating this amount into the analysis, the net benefits of preserving the study area are still positive when using the mean benefit measure from the contingent valuation study. Thus, direct employment values are still not enough to outweigh the benefits.

If one also includes indirect employment benefits, then the results change. Indirect employment is typically assumed to be 3 to 4 times the value of direct employment. These values outweigh the benefits of American marten preservation by a large amount. However, one should recognize that these values become relevant to the analysis only under very specific conditions. Clearly, if alternate sources of timber are available, these indirect benefits disappear. Even if alternate sources of timber are available but at higher costs, this situation will dramatically reduce the indirect values associated with this particular area of land.

The result of our heuristic, yet hopefully instructive, benefit-cost analysis of the American marten study area is that if one considers only direct benefits associated with timber production versus net benefits of the habitat conservation program, the habitat program is acceptable on economic efficiency grounds. If one includes direct employment benefits as well as direct benefits of forest harvesting, the study area benefits still outweigh the forest development benefits. Only if one includes all direct and indirect benefits of forestry activity is the use of the land in forestry supported on an economic efficiency basis. The latter approach is considered untenable by most economists, but is often used in various public debate forums. We must now consider the merits and drawbacks of the economic efficiency approach and the use of non-market valuation in this context.

Economic Analysis - Caveats

The analysis presented above assesses the benefits associated with an American marten preservation area against the benefits of using the area in commercial forestry. There are 3 forms of caveats that must be examined: (1) the potential complementarities of forestry and marten habitat, (2) issues surrounding the use of economic efficiency as a decision framework, and (3) the implications of using approaches like contingent valuation for measuring benefits.

The benefit-cost analysis described above suggests that American marten preservation and forestry activity are mutually exclusive. This exclusiveness may not be the case. If there are harvesting approaches and management

techniques that allow for the maintenance of habitat as well as timber production, then these alternative management scenarios should be examined. We assume, essentially, that forest harvesting and American marten objectives are directly conflicting. The analysis could be redone with any combination of these activities; however, the calculation of benefits and costs would be much more complex.

A second area of concern is the use of economic-efficiency criteria in land use planning. Should examination of the benefit-cost ratio be the sole criteria in management? The answer is almost always "no." Although economic efficiency can be considered one goal, there are many other social objectives that need to be considered. We have extended typical economic analysis to include values for non-market goods, and thus have extended the approach used in most economic-efficiency analyses; however, this is not the last word. In addition to efficiency, one must consider equity goals, both intragenerational and intergenerational.

Intragenerational equity considerations include concerns about the distribution of income or wealth (market and non-market) over individuals in our current society. Decisions about land use typically include some consideration about who benefits and who loses from the decision. In our case study, the issue would surround the distributional impact of employment benefits, for example, and the incidence of the environmental benefits realized from the American marten study area. These issues are clearly about collective or social choice, and economic analysis can only provide input into these social decisions.

Intergenerational equity refers to the assessment of distribution of goods and services over time (or over generations). If the American marten does not exist in the future, then future generations may suffer because of this loss. Economists typically use discount rates to convert future benefits to present values (although discounting environmental benefits is still somewhat controversial; see Price 1993). In this case study, the question becomes – can values for environmental goods and consumer goods (timber products) be discounted at the same rate, or, are values for environmental goods and consumer goods changing at different rates through time? One could hypothesize that environmental values are growing more rapidly than values for consumer goods, implying that adjustments be made to account for this intertemporal difference in values.

The final set of caveats relates to the use of contingent valuation in this type of analysis. The accuracy of the technique in eliciting values has been a question examined by many researchers. In this case there may be other benefits associated with a preservation area that are not captured by the contingent valuation question. Alternately, it may be that individuals are valuing more than the American marten in their responses and to attempt to value individual components of the ecosystem and combined responses would be double counting (Bishop and Welsh 1993).

Contingent valuation mimics a political decision-making process in which the issue is put to a referendum. Thus, we have already assumed a collective choice structure, direct democracy, that is different than our normal route, representative democracy. The reason that this route is chosen is that direct democracy is very similar, in construct, to market behavior. In a market system, individuals make choices and these choices are translated into prices (or measures of value) and are used as signals in the economy. Referendum democracy operates in a similar manner in that each individual makes a choice and sends a signal, rather than having decisions made "on their behalf" by a set of elected officials. There are advantages and disadvantages associated with these decision-making structures (e.g., van den Doel and van Velthoven 1993), and the debate quickly involves politics and political mechanisms, in addition to economics. It should be noted, however, that the political and economic aspects of the problem are inseparable. We are dealing with a collective choice problem (not a choice of a market good) and thus the mechanism of collective decision making (politics) and the economic aspects of the problem become intertwined.

The use of mechanisms like contingent valuation raises all of the problems associated with polling, referenda and voting. Issues like voter information, voter apathy, strategic voting, etc. become concerns for the analyst. The values revealed through this technique are endogenous to the political structure, and thus it should be clear that it is impossible to separate the economics from the politics.

Conclusions

Traditionally, species like marten have been valued for their fur. Since there is a well-developed market for fur, this value is relatively easy to discover and use in resource-allocation decisions and land-use decisions. However, relative to other land uses, the market value of fur is quite small, almost insignificant. In this paper, we have outlined other "values" associated with species like marten. They have value in that they play a particular role in an ecosystem and may be a critical species in some ecosystems. These values are "public goods" characteristics in that no one individual can capture the value of a wilderness, for example, but society benefits from the existence of wilderness areas. Martens may have considerable value that is not reflected in the market place and is identifiable only through social science research that simulates collective decision-making processes. Alternatively, the marten is part of the ecosystem or wilderness area toward which people attribute existence value. Existence values and other passive use values are becoming more important in economic analysis and in resource-use decision making, partly because of the development of techniques to identify these values, and also because the values themselves may be on the rise.

In the case study, we identified the benefits and costs of an American marten conservation program. Although this study is relatively simple, it acts to identify the components of an analysis of this type. Accurate biological information on the species as well as the other land uses (forestry) is essential for proper analysis. Also, the potential complementarities between land uses should be examined in the search for an optimal management strategy. The economic analysis relies on careful structuring of the biological information and presentation of the implications of alternative management options on the biological, economic and social environment. Finally, some form of collective choice structure is used to understand the tradeoffs that society is willing to make, or effectively, the value associated with the various options. In our case, we chose contingent valuation, which resembles a referendum approach, to examine these tradeoffs. This approach is not without its problems, but recognizing its weaknesses and its role in economic analysis is important in order to define future research agendas.

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SILVICULTURAL SYSTEMS FOR MAINTAINING MARTEN AND FISHER IN THE BOREAL FOREST

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Abstract: *Martes* species common to the boreal forest are adapted to structurally diverse plant communities. This diversity is largely due to the differences in forest composition and structure that are common as stands redevelop following disturbance, usually from forest fires. Shade-intolerant, early successional species such as aspen (*Populus tremuloides*) or pines (*Pinus* spp.) usually recruit immediately after fire, whereas more shade-tolerant species such as white spruce (*Picea glauca*) and balsam fir (*Abies balsamea*) establish gradually as the stand develops. Even-aged aspen and pine are gradually replaced with uneven-aged multistoried mixtures dominated by spruce and fir. Currently, even-aged management and clearcut harvesting systems have been used almost exclusively to regenerate boreal forests. This approach results in simple forests of aspen or pine, or if planting and vegetation management techniques are used, relatively pure stands of spruce. There are, however, other silvicultural systems that might be used to produce forests that are uneven-aged and multi-storied, conditions that are more typical of older forests and are more favorable to American marten (*Martes americana*) and fisher (*M. pennanti*). Shelterwood (harvesting) systems remove the mature trees through several partial cuts while simultaneously regenerating an even-aged stand of shade-intolerant species in the understory. Selection systems produce uneven-aged forests. These systems require periodic entries into the forest to remove part of the overstory to stimulate recruitment of more trees after each cut. Thinning treatments result in more space between trees, which increases light and other resources for understory trees, shrubs and herbs, thereby increasing the diversity of this lower layer. Thinning might also be used to prolong rotations or speed the growth of trees to promote old-growth structures.

Introduction

Silviculture can be defined as activities that control regeneration, species composition and structure of the forest. It has also been described as "applied ecology" (Smith 1986), where the knowledge of the way that trees and other forest species develop over time can be used to direct the stand's future structure and

composition. Over the years, emphasis has been placed on maximizing wood fiber production in the most efficient ways available. Generally, silvicultural treatments have aimed at establishing homogeneous plantations of genetically superior trees following clearcut logging. Although this management strategy is defensible from the perspective of fiber production, there is concern that these forests will not yield the same diversity and wildlife benefits as the original wild forest (Hunter 1991). This concern is particularly valid for the American marten (*Martes americana*) and fisher (*M. pennanti*), which are generally considered to be old-growth species (Buskirk and Powell 1994, Buskirk and Ruggiero 1994, Powell and Zielinski 1994).

In this paper, we briefly discuss the effect of stand structure on marten and fisher, and the stages of natural stand development following stand-replacing fire disturbances. But the major purpose of this paper is to discuss the spectrum of silvicultural systems that might be applied to the boreal forests of Alberta and discuss the effects of these treatments on composition and structure. As this topic is much too broad for a complete treatment, our basic goal was to introduce wildlife scientists and managers to some of the silvicultural systems available to forestry decision makers and how these systems might be used to enhance forests for both wildlife habitat, specifically for *Martes*, and wood production. The nomenclature for the flora follows Moss (1983).

Forest as Habitats

In the future, ecosystem management will require better cooperation among all resource managers. Specifically, on public forest lands, managers will have to ensure that their programs provide for "semi-natural" conditions (Rowe 1992, Lieffers and Beck 1994), "biodiversity" (Burton et al. 1992) and wildlife habitats (Black 1985, Christie 1988). It may not be easy to describe or fulfill the objectives of such theoretical concepts as maintaining semi-natural conditions or biodiversity of wildlife habitats. However, it is possible to do more than is currently being done. The first step is to realize that any management intervention that tries to simplify natural communities and processes in the boreal forest will result in less habitat for the indigenous plant and animal species. Presumably all of the natural stages of stand development are important as habitat for specific species of wildlife in the boreal forest.

Marten and fisher are 2 species found in the boreal forests of Alberta. In general, older treed habitats are preferred because crown closure provides protection from avian predators and the increased cover provides escape from larger mammalian predators. Downed and dead logs and standing snags are also common in older stands, and they are frequently used as resting sites or natal cover. Also, these older stands provide the habitat needed by prey species upon which these

2 species depend (Martin 1994). In general both species seem to benefit more from highly diverse habitats or a variety of microhabitats within older stands (Buskirk and Powell 1994, Buskirk and Ruggiero 1994, Powell and Zielinski 1994). This benefit probably occurs because both species have catholic diets, and habitat diversity contributes to variety and availability of food resources.

Timber harvesting is considered to be the primary cause of habitat loss for both marten and fisher (Douglas and Strickland 1987; Thompson 1988, 1991; Buck et al. 1994; Thompson and Harestad 1994). In general, clearcut harvesting tends to reduce habitat diversity because it is applied to older stands first, and it removes the canopy cover, which is important for survival of both species. In the absence of habitat suitability models (Verner et al. 1986) for treed plant communities in Alberta's boreal forests, managers are practicing "coarse filter management" (Hunter 1991) in the hopes of minimizing their effects on marten, fisher and other animal species found in these stands. At present this practice involves clearcutting in the shapes of natural disturbance patterns, leaving a small amount of residual canopy intact. Given existing legislation and contractual or economic restrictions, it may not be possible to develop the complete range of stand types and ages in a given area using this system. However, we must take advantage of the knowledge of silvicultural systems in the development of diverse wildlife habitats and demand that silvicultural manipulations of stands consider wildlife as well as the wood production concerns.

Natural Stand Development in Northern Forests

Following stand-replacing disturbances such as fire, mesic sites of northern forests are dominated by shade-intolerant hardwoods such as aspen (Heinselman 1981). This shade-intolerant species resprouts prolifically from root suckers (Schier 1973), demands full light intensities for optimum growth, has fast juvenile growth and quickly dominates open sites (Peterson and Peterson 1992). Aspen forests, however, have a thin canopy (Lieffers and Stadt 1994) that allows the development of a rich shrub/herb understory and the establishment of shade-tolerant white spruce and balsam fir. After some decades, the stand becomes distinctly 2-layered with an aspen overstory sheltering a growing understory of spruce and fir (Achuff and LaRoi 1977) (Fig. 1A). The long life and the tall stature of the white spruce and fir allows them to equal the height of the aspen (Fig. 1B) and eventually dominate the site after 70 or more years in the understory.

The relatively even-aged and full-grown spruce and fir are shade-tolerant species and have tall and dense crowns (Fig. 1C). This canopy results in reduced light transmission to the lower layers of the forest, and as a result there are fewer shrubs, forbs and grasses found in their understory and there is little establishment

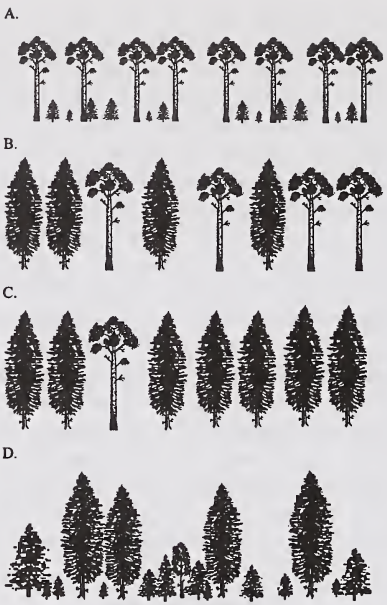

Figure 1. Stages of stand development in the boreal mixedwood forest. (A) Aspen overstory with developing spruce/fir understory. (B) Spruce/fir reaching the same height as the aspen. (C) Relatively even-aged spruce/fir overstory. (D) Uneven-aged spruce/fir forest.

of tree seedlings. This stage has been described as the "stem exclusion phase" of stand development (Oliver and Larson 1990). This stage is usually the time of maximum wood biomass (Bormann and Likens 1979), and it is frequently the time when clearcut harvesting is applied. If the stands are left to develop further, the mature trees gradually die. This loss creates gaps in the overstory that allow understory trees to develop. This has been described as the "understory re-initiation phase" (Oliver and Larson 1990). These young trees gradually take on more prominent positions in the canopy, and over time an all-aged and multi-layered canopy can result. This result is particularly likely if there are repeated minor disturbances in the stand that kill some of the trees and allow recruitment of more trees (Fig. 1D). This last stage of stand development is relatively unusual in the boreal forest because most stands are destroyed by fire before reaching

this stage (Murphy 1985). This uneven-aged phase of stand development is also called the "old-growth phase;" however, there are other definitions of old-growth forests (Hunter 1991).

Silvicultural Systems

There are 2 principal types of silvicultural (tree regeneration) systems: even-aged and uneven-aged. An even-aged stand is a forest where the range of ages of the trees is within 10 to 20 years of the mean age for that stand. Lorimer (1990), however, states that in mature even-aged stands, the actual range of ages is frequently 20 to 30 years. Uneven-aged stands have three or more age classes and the term "all-aged" is used when there is nearly continuous recruitment of trees into the stand.

Even-Aged Systems

Clearcutting is the complete removal of the forest canopy in one cut (Smith 1986). The period between harvests is called the "rotation." Following clearcutting, all of the growing space is open for colonization by all species with viable seed; however, sites are usually dominated by fast-growing, sun-loving early successional species. In the boreal forest this species is usually aspen, or balsam poplar (*P. balsamifera*) on wetter sites, or shrubs or grasses such as marsh reed grass (*Calamagrostis canadensis*). Frequently clearcutting is also used to initiate a new stand of more shade-intolerant species such as white spruce. Here, the site is usually given some site preparation treatment to provide suitable planting sites and to improve planter access. Planted spruce do not have fast juvenile growth rates and are usually overtopped by early successional species (Nienstadt and Zasada 1990). Mechanical or chemical vegetation control measures are usually applied to allow the coniferous species to achieve a dominant position in the developing canopy. Depending on the success of the planting stock and the vegetation control, the resulting stand will be even-aged with a mixed canopy of hardwoods and conifers, if competition to the conifers is not controlled, or it could be a relatively uniform and pure stand of conifers if vegetation control is applied.

Shelterwood systems gradually remove the canopy of a mature stand in a series of cuts, thereby freeing up growing space for the establishment of the next generation of trees (Matthews 1989). In the first cut, 30% to 60% of the overstory might be removed leaving approximately 16 to 22 m^2/ha. This system develops a relatively even-aged stand in the understory (Fig. 2A) and it is best suited for establishing those species that do not need full sunlight for growth, or those that would benefit from shelter. Species such as spruce and fir fit this category. These understory trees may establish from planting or natural regeneration.

Figure 2 (A) Seeding cut of shelterwood system. (B) Spruce/fir and aspen mosaic following careful logging of mature aspen and "protecting" the spruce/fir understory.

This series of cuts may last 20 years, and the canopy structure becomes distinctly 2-layered during the regeneration period; there is an open canopy of dominant, mature trees and a developing understory layer. Shelterwood systems can largely bypass the early successional stages of stand development by eliminating the stage of completely open conditions with full light necessary for the domination of shade-intolerant species. Once the regenerated trees no longer require the sheltering trees to moderate the microclimate or the regenerated trees are tall enough to be above competing vegetation, the overstory trees may be removed. The composition of the stand at this time is likely similar to that of plantations where competing vegetation has been controlled.

Understory protection systems in the boreal forest are a form of natural shelterwood in which mature aspen stands with an understory of white spruce (Fig. 1A) are carefully logged to remove the aspen but leave the understory spruce undamaged (Brace and Bella 1988). The resulting stands are quickly dominated by the "protected" white spruce, but aspen resprouts on access trails and extraction roads, which are common after logging. The result is a two-aged white spruce and aspen stand where the species occupy separate but contiguous areas within the same cutting area (Fig. 2B). This structure is somewhat similar to that following a fire, which commonly leaves strips of living timber within burned areas. There is also the possibility of planting spruce in the understory 10 to 20 years prior to the maturity of the aspen. This underplanting will establish under the aspen overstory a stratum of spruce which can be saved during careful harvest of the aspen.

Seed Tree systems leave dominant, well-spaced, well-formed trees either singly or in clusters over a cutover in order to provide seed to regenerate the next stand of trees. These seed trees are considered to have little effect on the microclimate of the cutover. For seed tree systems to be successful, the trees must be windfirm and the site must not be colonized by extremely competitive species. Spacing of the remaining trees varies by species, their height and the direction of the prevailing wind (Greene and Johnson 1996). The seed trees can be harvested once their progeny become established, or these mature trees might be left as reserve trees to provide structure to the forest during the next rotation. With long-lived species, these trees may live long enough to reach the next harvest and provide wood of exceptional size and value, while increasing the structural diversity of the stand throughout the rotation.

Uneven-Aged Systems

Single Tree Selection is an uneven-aged management system (Smith 1986, Nyland 1996) that is commonly used in the shade-tolerant hardwood forests of eastern North America. In these forests, there is a wide range of ages and sizes represented in a single stand; it is comparable to the natural all-aged forests that develop on very old spruce-dominated sites in the boreal forest (Fig. 1D). Single tree selection is usually accomplished by frequent harvests. The period between harvests is called the "cutting cycle." At each of the harvests, there should be enough trees removed such that sufficient growing space is created for the recruitment of more trees. This usually requires the stand density be lowered to 50-70% of the maximum growing stock for this type of site. If too many trees are removed, then there is a significant loss in overall stand productivity because not all of the growing space is occupied. If too few trees are removed, there will be little recruitment of new trees. Historically, single tree selection meant cutting the largest and highest quality trees. This system became known as "high grading" and the process significantly lowered the genetic quality of the residual growing stock. More recently, single tree selection systems attempt to maintain many small trees with fewer and fewer larger trees, which results in a negative exponential or reverse J-shaped size-frequency distribution. However, there is little reason for maintaining this reverse J structure, and as a result, many foresters are advocating density control through the removal of trees in a variety of size classes. The emphasis now is on optimizing the use of the growing space. The resulting stand structures are similar to the idealized uneven-aged stands of old-growth forests in that there is a range of size classes represented and lower total wood biomass, and the overstory canopy is irregular both horizontally and vertically. The individual tree selection systems are well-suited to regenerating shade-tolerant species and in Alberta have been most successfully applied by small landowners. It is an intensive management system that requires skill and planning.

Although this system appears to be idyllic, stands under a single tree selection system must be more frequently disturbed (cut), which usually requires a greater network of access/extraction trails. Also, there is usually greater damage to residual trees due to felling and skidding. In general, harvesting costs are highest with this system.

Group Selection removes patches of forest up to 2 tree heights in diameter at each cutting cycle (Nyland 1996). At high latitudes these holes in the canopy produce highly variable conditions; on the southern edge of the canopy opening, the area is heavily shaded, whereas the northern edge of the opening receives full sunlight for much of the day. This variation provides habitat for both shade-tolerant and intolerant species in a relatively confined space. Relatively even-aged patches of forest are created but the entire spatial mosaic of the area affected by this system should be classed as "uneven-aged." Forests managed under group selection are spatially highly variable in that there are old and young trees, and tolerant and intolerant trees in close association. These stands have a large amount of structural diversity and edge.

Other Silvicultural Treatments

Thinning is the removal of some of the trees in a stand to provide growing space for the development of the remaining trees. Very large increases in the size of individual trees can result from thinning a stand. Self-thinning (i.e., tree mortality associated with competition with other trees, even of the same species) will occur naturally, but in most circumstances will occur over a much longer time period than artificial thinning (Drew and Flewelling 1979). Although thinning is usually applied to a stand to increase growth rates, size, and usefulness of the trees for wood production, it can also be used to speed the development of individual stands for other reasons, such as wildlife habitat enhancement. For example, very dense stands of trees, which are known to result from disturbance, may be stagnant and have a very sparse understory. Thinning can be used to open up these stands, encouraging the development of understory communities. Second, a characteristic of old-growth stands is large, well-spaced trees. This feature could be achieved more rapidly by thinning stands to promote the rapid development of large trees (Oliver 1992). Third, if the stand is composed of trees that are long-lived and have potential for increased growth at an older age when competition is reduced, then crown or selection thinning might be applied. Here some of the larger trees in the site might be cut to promote the growth of healthy, smaller trees. This practice will extend the life of the stand and keep older stands in the landscape for a longer period of time. The residue from these programs is left on site, and conditions for certain wildlife species may be improved.

Pruning removes branches in the lower part of the bole of the tree. The branch of a tree will produce a knot in the wood where it attaches to the trunk. Once the branch is completely removed the tree will put on only clear wood over the former branch position. Older forests frequently are self-pruned because of natural branch death and removal of branches through physical or fungal agents. To improve wood value, pruning is done in younger stands to produce trees that do not have lower branches. Because part of the canopy is removed, however, more light is transmitted to lower layers and understory layers are better developed in pruned stands. On the other hand, pruned stands will have a more restricted and uniform crown layering.

Management Considerations

Silvicultural systems were originally designed to ensure the continuous supply of high-quality wood fiber from the forested land base. As part of this goal, silvicultural research has emphasized methods that shorten rotations and cutting cycles, lower regeneration costs, lower fire protection costs, reduce losses due to insects and diseases, and still produce high-value wood fiber. Little emphasis has been placed on using silvicultural information to produce other goods and services. However, the public is now demanding that foresters assume the responsibility of maintaining the biological integrity of the forest, and the natural processes and biodiversity that occur throughout stand development.

It is extremely difficult to describe or prescribe the strategies required to maintain all social goods and services from the forest. This would be true even if we were to restrict our goal to producing marten and fisher habitat. Instead, it is our hope that wildlife managers will use the information given to constructively dialogue with foresters who will likely use the techniques described above to produce or maintain conditions required by marten and fisher. As discussed earlier, both species benefit from diverse habitats, particularly those stands that have well developed overstories and complex understories where downed woody debris and surface vegetation are available. These forest features have not been managed for in the past, but they can be accomplished if these goals are identified and accepted as part of the management plan for an area. In conclusion, there are new ways of practicing intensive forestry that are more natural than those used in the past (Lieffers et al. 1996). As wildlife managers become more aware of the tools available to them they will be better able to plant the seeds of change.

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SIMULATED SPATIAL DYNAMICS OF MARTENS IN RESPONSE TO HABITAT SUCCESSION IN THE WESTERN NEWFOUNDLAND MODEL FOREST

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Abstract: I constructed a model of American marten (*Martes americana*) population dynamics and used it to investigate the spatial dynamics of martens in the Western Newfoundland Model Forest. The model was based on rules governing the behavior and physiology of individual martens and it incorporated demographic and environmental stochasticity. Spatial dynamics of the population were explicitly linked to a digital vegetation map of the study area. The primary outcome was the probabilistic distribution of the population 75 years from the present, relative to various combinations of model parameter values. Over 75 years the modeled population moved to a region of regenerating forest to the northwest of its current range. The current range was completely abandoned in most simulations. Parameter settings that resulted in larger population sizes also resulted in a wider area of distribution and a higher overall probability of occupancy per site, but the region of highest relative use was essentially constant. When accidental trapping mortality was added to the model, a rate of only 10% per annum was sufficient to restrict the population to a region where all trapping is currently prohibited. The relative quality of the various habitat types present and how they will change over time were identified as primary issues for further empirical research.

Introduction

The Newfoundland American marten (*Martes americana*) population has been declining in number and distribution since the early 1900's and was assigned "threatened" status by the Committee on the Status of Endangered Species in Canada (COSEWIC) in 1986 (Burnett et al. 1989). Numerous factors have been implicated in the decline of the population including over-trapping, habitat loss, disease epidemics, and the depauperate prey base on the island (Bissonette et al. 1988). The trapping season for martens was closed in 1934; however, animals are still accidentally killed in traps set for other species and in rabbit snares (Canadian-Newfoundland Marten Recovery Team [CNMRT] 1995). The remaining martens are now concentrated in the southwestern part of the island, in the Grand Lake - Little Grand Lake region (Bissonette et al. 1988). It is estimated that fewer than 200 animals remain (L. Mayo, Newfoundland Wildlife Division, Newfoundland, pers. comm.).

The major problem facing the Newfoundland marten population in the immediate future is habitat availability. It has been hypothesized that because of an imbalance in the forest age structure resulting from forestry operations, suitable habitat for martens in Newfoundland (i.e., older age classes) will be in short supply 30 to 50 years from now (Thompson 1991). Although martens in Newfoundland are protected, their habitat is not.

A recovery plan has been developed for the Newfoundland marten population. In it, a key recommendation is to immediately protect habitat in the current core range from further timber harvesting and to designate an additional reserve area that will eventually be suitable for martens as the habitat matures (CNMRT 1995). Habitat use, particularly for small populations, is a function of habitat availability and population processes, so both of these factors should be taken into account when determining where the new reserve will be located. For example, on a local scale the territorial behavior of martens precludes the use of small isolated patches of habitat, even if they are of high quality, and therefore these patches do not contribute to available habitat (Buskirk and Powell 1994). On a landscape scale, the intrinsic growth rate of the population and the viability of dispersing animals play a critical role in determining how far (or even if) a population can move across the landscape to utilize new habitat as it becomes available over time.

In a previous investigation, I constructed a spatially explicit model of marten population dynamics and used it to conduct a population viability analysis for the Newfoundland marten population (Schneider, unpublished manuscript). In this investigation I conducted further simulations to address the question: in the absence of further timber harvesting, where would the marten population preferentially be located 75 years from the present? My intent was to provide information that would be useful in making a decision on reserve site designation. Seventy-five years was chosen as the endpoint because it immediately follows the period of projected habitat shortage that will force the marten population to move from its current core range (Thompson 1991). The explicit linking of population dynamic models with geographic information system (GIS) databases is a recent undertaking and there are few examples of such models in the literature. It was also my intent to provide an example of a workable approach to this type of modeling.

Study Area

The study area was defined by the boundaries of the Western Newfoundland Model Forest (WNMF) (Canadian Forest Service 1994). The WNMF covers 707,060 ha and is bounded by Gros Morne National Park on the north, the Buchans Plateau and Lloyd's river on the east, the Burgeo highway on the south

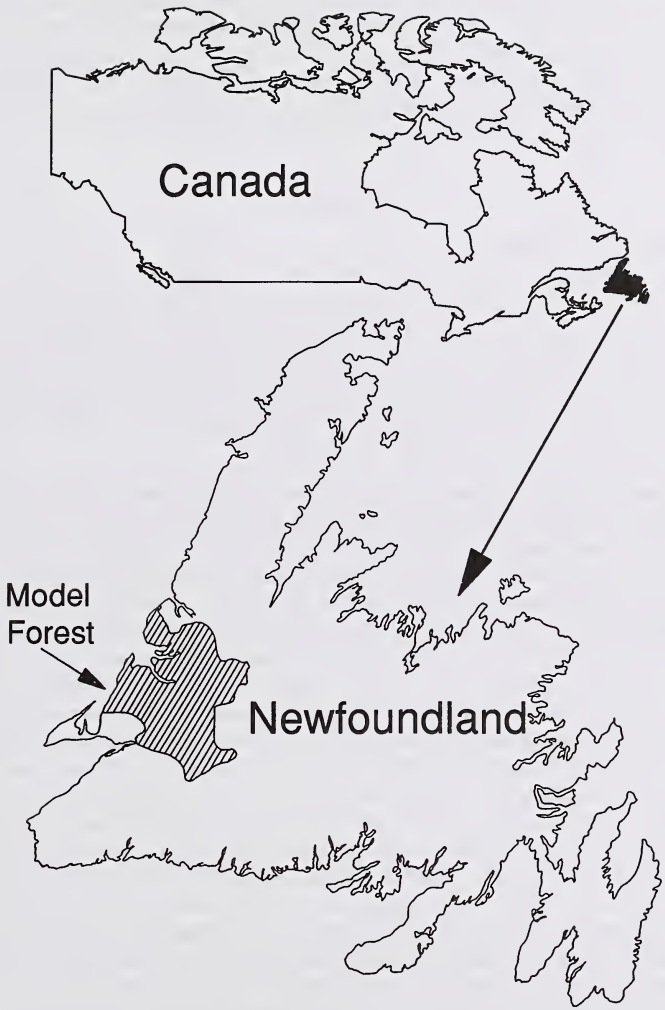

Figure 1. Location of study site (shaded) in Newfoundland, Canada.

and the Gulf of St. Lawrence on the west (Fig. 1). Fifty percent of the area is productive boreal forest, and softwood scrub, bogs, rock barrens, and water account for most of the remaining area. Balsam fir (*Abies balsamea*) is the dominant tree species (90%); black spruce (*Picea mariana*) and white birch (*Betula papyrifera*) are also present. Two forest-product companies harvest timber from the area with a combined annual allowable cut of 296,000 m^3 (WNMF 1991).

Methods

Model Construction

A review of the literature was conducted and a set of rules describing the essential features of marten demography at the individual-animal level was compiled (see Appendix). Using these rules, an individual-based model running in discrete time steps of 1 year was constructed. Only the dynamic behavior of females was followed, based on the assumption that the population would always contain enough males to breed all females and that males do not compete for territories with females (Strickland and Douglas 1987).

A central concept in the model was that of an optimum territory size (OTS: the amount of territory required to ensure access to sufficient prey to meet all energetic requirements, including reproduction). The OTS was used as a proxy measure for prey availability, integrating the influence of habitat type (territories are larger in poor quality habitat; Soutiere 1979) and annual variations in prey density (territory size is inversely proportional to prey density; Thompson and Colgan 1987). I assumed that all martens strive to reach the OTS but do not exceed it because of the energetic costs involved (Thompson and Colgan 1994).

A raster vegetation map (current to 1992) with a resolution of 6.0 ha per cell was used to link the model to the habitat of the study area. Cells containing forest were categorized into 7 habitat types corresponding to 20-year age classes. It was assumed that prey availability would differ among the habitat types and therefore the OTS parameter was defined separately for each (Table 1). By utilizing a point system to relate the habitat types (conceptually corresponding to the number of prey items provided per cell of habitat), the percentage of OTS present in territories comprised of multiple habitat types could be calculated.

Forest stands in Newfoundland generally revert to new growth after 120 years of age because of insect damage, wind throw and other processes (Thompson 1991; B. Pittmann, Western Newfoundland Model Forest Inc., Newfoundland, pers. commun.; G. VanDusen, Corner Brook Pulp and Paper, Newfoundland, pers. commun.). In the model, all cells in the vegetation map composed of forest were aged at 5-year intervals and cells in the 120-140 year age class were probabilistically converted to the 0-20 year age class over a period of 20 years.

Table 1. Habitat quality parameters, including base model estimates and the maximum and minimum values used for sensitivity testing.

Habitat quality by age class (%)[a]	Base model estimate[b]	Minimum	Maximum
0-19 years	0.0	0.0	0.0
20-39 years	10.0	5.0	20.0
40-59 years	45.0	25.0	60.0
60-79 years	75.0	50.0	100.0
80-99 years	90.0	75.0	100.0
100-119 years	100.0	100.0	100.0
120+ years	90.0	80.0	100.0

[a] The habitat quality parameters refer to the percentage contribution, in terms of prey availability, of each habitat type relative to the reference optimum territory size class (100-119 years).

[b] Parameter estimates derived from Thompson and Harestad (1994).

Fluctuations in the prey base constitute the major source of environmental stochasticity for martens (Weckwerth and Hawley 1962). This factor was again modeled using the OTS concept under the assumption that, for each habitat type, annual fluctuations in prey density are reflected in annual fluctuations in OTS. The stochastic pattern of annual fluctuations in OTS was defined in the model by a sequence of random numbers within a specified range (Table 2). The fluctuations were uniformly applied across the study area as a percent deviation from the long-term mean OTS for each habitat type.

The computer model consisted of sequential modules for spatial dynamics, reproduction and mortality. The module for spatial dynamics simulated an annual competition for the establishment of territories among females. Each female would attempt to acquire 100% of the OTS as determined by the habitat types available to her locally and by the current prey density (see Appendix). Resident females, as the best competitors, were given first opportunity to establish territories, followed by transient adults and then juveniles. Within each of these groups territory acquisition was simultaneous and incremental among all females.

Each female would begin the competition with 1 6.0-ha habitat cell, representing its core area from the previous year. If it was unable to establish a minimum territory locally because of the presence of conspecifics or unsuitable habitat, it was given the opportunity to disperse to a patch of unoccupied habitat. Dispersal was in an outward spiral from the core cell starting in a randomly assigned direction. Females that were unable to find suitable habitat within a specified distance (Table 2) were placed in the transient class for that year. The

Table 2. Model parameters, including base model estimates.[a]

Parameter	Base model estimate
Maximum litter size[b]	3.1
Minimum % OTS[c] for reproduction[b]	25.0
Maximum dispersal distance (km)	20.0
Adult resident mortality rate	0.35
Adult transient mortality rate	0.60
Juvenile mortality rate	0.55
Reference OTS (km^2)[d]	4.0
Minimum territory size (% of OTS)	25.0
Maximum territory size (km^2)	12.0
Environmental stochasticity[e]	3.0

[a] The values represent pooled estimates from the studies cited in the Appendix. All rates refer to a period of 1 year.

[b] Reproductive parameters control litter size according to the function illustrated in Figure 2.

[c] Optimum territory size

[d] The reference OTS refers to the estimated long-term mean OTS in a homogeneous patch of the highest quality habitat.

[e] Long-term maximum OTS divided by long-term minimum OTS.

limits of the study area acted as a reflecting boundary for dispersers; however, this result was an infrequent occurrence because of the large size of the study site.

Reproduction for each female was modeled as a function of energy (i.e., prey) availability, again using the proxy measure of OTS (Fig. 2, Table 2). To incorporate stochastic processes operating at the level of the individual, the actual litter size for each female was determined by Monte Carlo sampling of a Gaussian distribution based on the individual mean litter size calculated above.

In the final module a probabilistic determination of mortality was made for each individual. The mean probability of mortality was separately defined for adult residents, adult transients, and juveniles (Table 2).

Model Experimentation

The investigation centered on the spatial dynamics of the population. The outcome of interest was a probabilistic estimate of the distribution of the population

Figure 2. Functional relationship between litter size and percentage of optimum territory size achieved.

75 years from the present. This estimate was determined by repeatedly running the model and keeping a running tally of marten presence or absence at year 75 for every cell on the study site map. The record of cumulative marten occupancy was then displayed as a map of the probability of marten occupancy per cell.

Distribution maps were generated for a variety of combinations of model parameters. Each map was based on a minimum of 100 repetitions, excluding populations that went extinct prior to the 75-year endpoint (extinction was assumed when there were fewer than 10 females remaining). One hundred repetitions was sufficient to provide stable results (i.e., maps generated with different random number sequences appeared similar on visual inspection). The starting population for the runs was based on a spatially-defined estimate supplied by wildlife managers in Newfoundland in 1994 (n = 113; L. Mayo, Newfoundland Wildlife Division, Newfoundland, pers. commun.).

The parameter estimates used for the base model were derived from pooled estimates from the literature (Tables 1 and 2). The rate of juvenile mortality (0.55) was selected to provide a strong intrinsic rate of growth for the population (the actual value of this parameter has not been well quantified). To investigate the effects of different rates of recruitment on the spatial dynamics of the population, the model was also run with the rate of juvenile mortality equal to 0.60 and 0.65. Additional runs of the model were conducted using extreme values for the habitat quality parameters (Table 1), maximum dispersal distance (10 and 40

km), and degree of environmental stochasticity (1 and 4; units = long-term maximum OTS divided by long-term minimum OTS). The effect of doubling the starting population size was also investigated.

A subset of the study area was designated as the Pine Marten Study Area in 1973 and all trapping and snaring of furbearers in this region is prohibited. To investigate the effects of accidental losses through trapping on marten spatial dynamics, a region approximating the Pine Marten Study Area was defined in the model and various rates of additional probabilistic mortality were applied to martens dispersing out of this zone.

Results

The initial run of the model was used to generate a distribution map for the current marten population after 4 years of equilibration (Fig. 3). After 75 years, with model parameters at their base settings (Tables 1 and 2), the population had

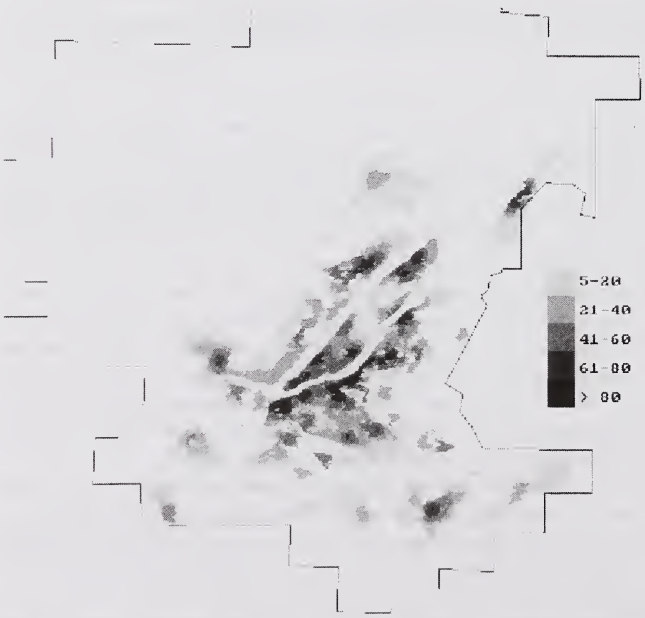

Figure 3. Probabilistic distribution of the marten population after initial equilibration (year = 4). Pixel shading is proportional to probability of occupancy (%).

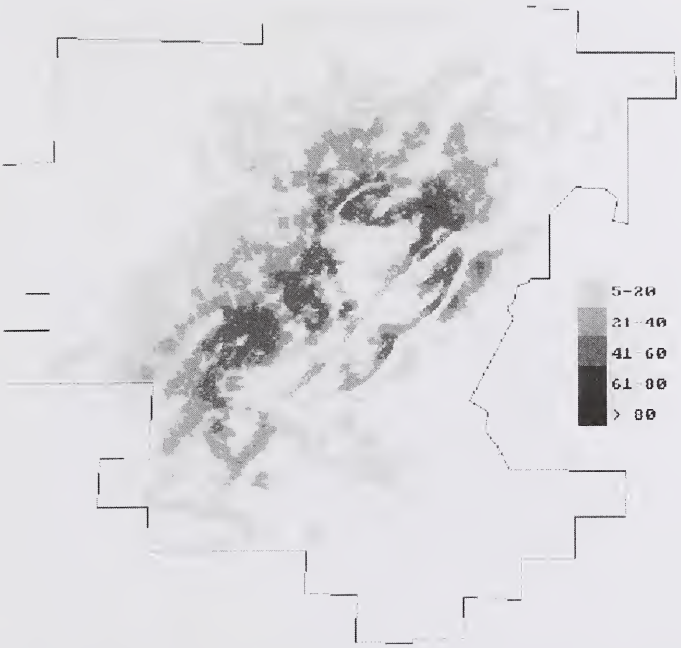

Figure 4. Probabilistic distribution of the marten population after 75 years using the base parameter settings (Tables 1 and 2). Pixel shading is proportional to probability of occupancy (%).

shifted to the west and north, abandoning most of its original range (Fig. 4). The population was distributed over a wider area and very few sites had more than a 60% probability of occupancy. The probability of extinction for this set of runs was 7.0% and the mean size of surviving populations at year 75 was 239.

When the model was run with the rate of juvenile mortality equal to 0.60, the basic pattern of distribution was similar but the overall probability of occupancy was reduced (Fig. 5). The rate of extinctions for this set of runs was 57% and the mean size of the surviving populations was 81. When the model was run with the rate of juvenile mortality equal to 0.65 all populations went extinct prior to 75 years.

Simulations with the habitat quality parameters at their minimum levels (Table 1) had a pattern of distribution similar to the base model runs but with an overall reduced probability of occupancy (Fig. 6). The rate of extinctions for these

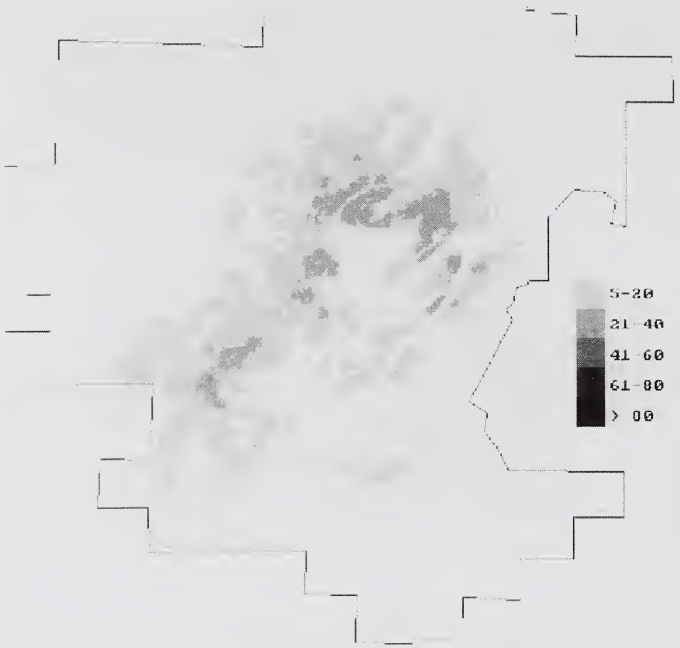

Figure 5. Probabilistic distribution of the marten population after 75 years using the base parameter settings (Tables 1 and 2), except that juvenile mortality = 0.6. Pixel shading is proportional to probability of occupancy (%).

runs was 92% and the mean size of surviving populations was 66. With habitat quality parameters at their maximum level (Table 1), the population was distributed over almost all of the forested region of the study site, but the region with highest probability of occupancy was still similar to the highest use region of the base model (Fig. 7). There were no extinctions in this set of runs and the mean size of surviving populations was 750.

Results from the other parameter combinations that were investigated fell within the range of patterns described above. Runs with reduced environmental stochasticity, larger maximum dispersal distance and larger starting population all resulted in larger mean population sizes at year 75 and greater overall rates of occupancy. The reverse was true for runs with higher environmental stochasticity and smaller maximum dispersal distance. Most of the changes were minor with the exception of runs in which environmental stochasticity was eliminated.

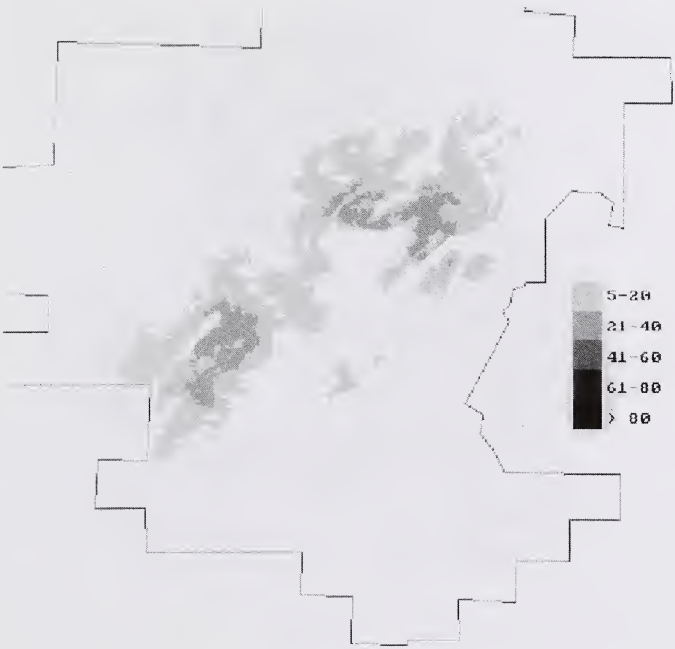

Figure 6. Probabilistic distribution of the marten population after 75 years using minimum settings for habitat quality (Table 1) and the base parameter settings in Table 2. Pixel shading is proportional to probability of occupancy (%).

In the runs incorporating mortality due to accidental trapping, the distribution of the population was progressively restricted as the rate of accidental trapping was increased. A rate of trapping mortality of only 10% per annum was sufficient to concentrate the population in the northwest quadrant of the Pine Marten Study Area (Fig. 8). With trapping mortality at 10%, the rate of population extinction was 36% and the mean size of surviving populations was 103.

Discussion

The data necessary for the explicit testing of the model's function in the current study area were unavailable. Therefore, the reliability of the results must be gauged on the basis of the assumptions on which the model was based, the parameter estimates used in the runs, and other applications of the model.

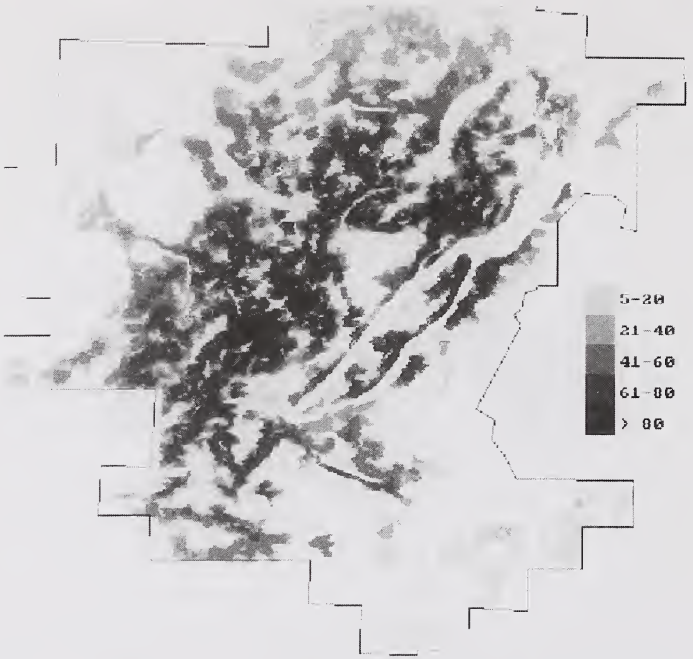

Figure 7. Probabilistic distribution of the marten population after 75 years using maximum settings for habitat quality (Table 1) and the base parameter settings in Table 2. Pixel shading is proportional to probability of occupancy (%).

Every attempt was made to incorporate as much biological realism as possible in the model, subject to our current state of knowledge on the species and technical limitations on the level of detail that could be incorporated. In a previous study using an earlier version of the model, the simulated age structure, temporal pattern of density fluctuations, and magnitude of density variations were all qualitatively similar to field data collected on natural populations in Ontario (Schneider and Yodzis 1994). Readers interested in an in-depth discussion of the construction and function of the model should refer to this earlier study. The major change in the current model was a refinement of the territory acquisition routine to produce territories in heterogeneous habitat that were qualitatively similar in size, shape and location (with respect to local habitat) to marten territories that have been mapped by telemetry in the Newfoundland study area (Mayo 1984, Bissonette et al. 1988).

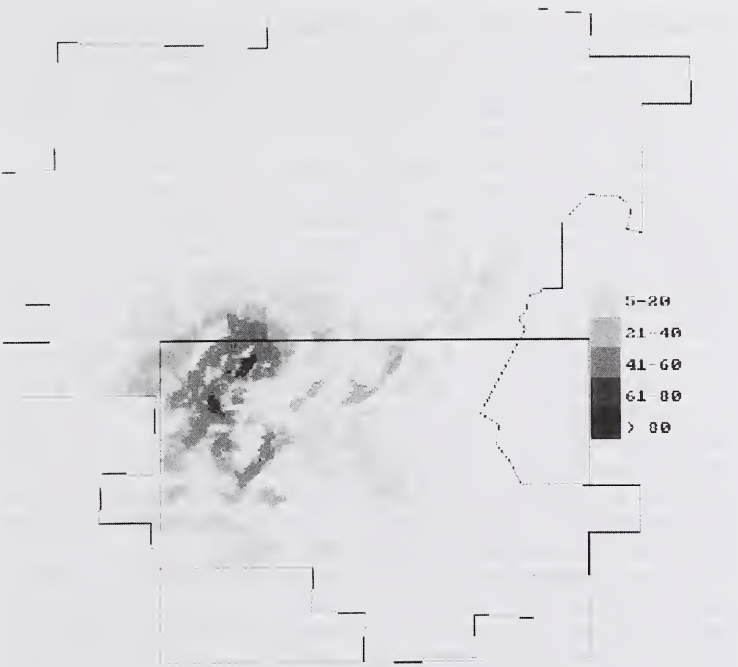

Figure 8. Probabilistic distribution of the marten population after 75 years using the base parameter settings (Tables 1 and 2), except that a trapping mortality of 10% was applied to martens that dispersed out of the Pine Marten Study Area (lower rectangle). Pixel shading is proportional to probability of occupancy (%).

The endpoint of 75 years was chosen because it captured the initial movement of the population after the projected deterioration of the current core range. Subsequent movements of the population will depend primarily on where the habitat reserve is located. The rate of juvenile mortality used in the base model was chosen to provide a strong intrinsic rate of growth for the population. This was because the investigation sought to determine where a *viable* population would preferentially relocate over time. The issue of population viability itself was the focus of an earlier study (Schneider, unpublished manuscript).

The results of the simulations support the hypothesis proposed by Thompson (1991) that habitat will become a limiting factor for the Newfoundland marten

population over the next 50 years. For all runs of the model there was a clear movement of the population over 75 years to the north and west of its current range (e.g., Fig. 4). The regions with the highest probability of use were consistent among the various simulations with the exception of runs incorporating trapping mortality.

Increasing the relative habitat quality settings enabled martens to use less optimal habitat and also led to an increase in the size of the population. Consequently, the area of distribution increased and the probability of use of individual cells was higher. Changes to other parameter values that resulted in a higher population growth rate also resulted in a larger area of distribution and higher overall probability of occupancy. For these runs population size and dispersal pressure were the main cause of the movement to less optimal habitat.

When an effort was made to count marten deaths in hare snares and traps from 1984-1988, the mean number was 14 per year (CNMRT 1995), which is equal to 5-10% of the population. Not all of the snaring losses can be expected to represent additive mortality; however, it is also unlikely that all of the snaring deaths were reported. When trapping mortality of 10% per annum was incorporated into the model, the population was largely confined to the Pine Marten Study Area (Fig. 8). The effect was pronounced because of the model's high sensitivity to the rate of juvenile mortality (Schneider and Yodzis 1994).

The issue in greatest need of further empirical study is the relative quality of the various habitat types available to the marten population and how this will change over time. The development of a habitat suitability index (HSI) model with an explicit link to marten reproduction would be a good approach to take (Lofroth and Banci 1991). A digital map based on HSI index values could then be substituted for the forest age-class map that was used in this investigation. A mechanism for projecting the HSI values over time, based on a better understanding of forest succession in the study site, would be necessary as well. Additional field research should also be focused on obtaining better estimates of basic demographic parameters such as the rate of juvenile mortality.

The data presented depict the projected implications of the best available information on the Newfoundland marten. They should provide an objective basis for deciding where to locate a habitat reserve for the population. This conclusion does not mean that the information used was complete or that some of the assumptions are not open to question. However, difficult decisions concerning forest harvesting must be made *today* if the marten is to benefit from additional information collected in coming years.

Provision must also be made for wide corridors where forest harvesting and all trapping and snaring are restricted. Without such restrictions, the simulations suggest that it is unlikely that the new reserve will be successfully colonized (Fig. 8). Furthermore, although we have maps and computers to help us project

habitat availability over time, martens have knowledge of only their local habitats to rely on. The "optimal" decisions concerning spatial movements, particularly for small populations where individual actions have a large influence, may not necessarily be made. Therefore it is possible that artificial transplantation will be necessary for effective colonization of the designated reserve area.

Since marten habitat is dynamic in time and space, a single reserve, unless it is extremely large, will not be adequate to maintain population viability. Therefore, a floating reserve system should be considered for the combined maintenance of a viable marten population (along with other old-growth dependent species) and a sustainable forest-products industry. As demonstrated in this investigation, the technology for this type of landscape-level planning is now in place; what is still needed is better empirical data and the political mandate to proceed.

Acknowledgments

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Appendix:
Biological Assumptions Used in the Construction of the Model

1. Martens maintain exclusive territories within each sex (Powell 1979).
2. Territory size is a function of prey availability (which is a function of local habitat quality and current prey density) and intraspecific competition (Weckwerth and Hawley 1962, Soutiere 1979, Fredrickson 1990). Martens will avoid incorporating low quality habitat into their territories; however, small features such as bogs and small clearcuts may be enveloped because marten territories cover such large areas (Snyder and Bissonette 1987).
3. There is a minimum limit to territory size set by the minimum quantity of prey necessary to meet maintenance requirements.
4. Martens unable to acquire the minimum territory size locally will disperse in search of suitable habitat elsewhere (Archibald and Jessup 1984). Suitable patches that are closer are given preference over patches that are farther away. If no suitable patches can be found within a given radius (Table 2) the individual will enter a reproductively inactive "transient" class for the year (Powell 1979, Thompson and Colgan 1987).
5. The energetic cost of territoriality, related to travel and cost of defence, is proportional to territory size (Thompson and Colgan 1994). As a consequence there is a maximum limit to territory size.
6. Martens compete annually for the establishment of territories. Residents have primary access to the available habitat (as the best competitors), followed by transients, and then young of the year (Weckwerth and Hawley 1962, Archibald and Jessup 1984, Bissonette et al. 1988).
7. Reproduction occurs only once per year, and marten females do not produce litters until they are at least 2 years of age (Strickland and Douglas 1987).
8. Males and females are born in approximately equal numbers (Strickland and Douglas 1987).

9. There is a physiological upper limit to the mean reproductive output for martens. Below that limit reproductive output is primarily a function of the energy balance of the female (Weckwerth and Hawley 1962, Archibald and Jessup 1984, Thompson and Colgan 1987, Bissonette et al. 1988).
10. The amount of energy available for reproduction is the amount derived from eating prey (primarily a function of prey availability) less a constant quantity for maintenance requirements and a variable quantity associated with territoriality.
11. In addition to the deterministic processes there are stochastic elements involved in reproduction reflecting processes operating at the individual-animal level (Simberloff 1988).
12. Mortality is primarily a stochastic process (Strickland and Douglas 1987).

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EFFECTS OF FOREST FRAGMENTATION ON POPULATIONS OF AMERICAN MARTEN IN THE INTERMOUNTAIN WEST

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Abstract: We compared relative population densities of American marten (*Martes americana*) across 18 sites that contained suitable marten habitat but differed in the degree of forest fragmentation from natural openings and timber clearcuts. These 9-km^2 sites were located in mature forests in the Uinta Mountains of northern Utah, and open areas occupied 2%-42% of each site. Our central question was whether marten populations would demonstrate a linear negative response to increased loss of forest cover, or if the increase in prey associated with clearcuts would improve habitat in sites with low to moderate levels of fragmentation. Relative marten densities were determined over 3 summers using 25 live-traps in each site for 6 consecutive nights. We estimated small mammal densities through a snap-trap survey and collected data on forest structure to examine their contribution in explaining variation in marten densities among sites. Landscape images were classified into 2 habitat types, forest and openings, using a raster-based geographic information system, and the percent of each site unforested was used as the measure of fragmentation. We found a significant ($P < 0.05$) negative correlation between marten captures and percent of the landscape in openings. Marten captures reached 0 when openings occupied >25% of the landscapes, indicating that marten populations may not persist in fragmented landscapes even though the forest habitat may still be contiguous. Marten densities were correlated with habitat quality, with high densities occurring in sites with breeding females, high body weights, good body condition, and overwinter success. Small mammal densities were significantly higher in clearcuts than in forests ($P < 0.001$), but marten captures were not correlated with the increase in number or biomass of prey associated with clearcuts. Southern red-backed vole (*Clethrionomys gapperi*) was the dominant species found in forests, whereas deer mouse (*Peromyscus maniculatus*) and least chipmunk (*Tamias minimus*) were the most frequent captures in clearcuts. Forest structural components were similar

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within all landscapes except for snag abundance, which varied considerably in relation to infestations of mountain pine beetle (*Dendroctonus ponderosae*). Because of the similarity in forest stand conditions, we found no correlations between marten captures and any component of forest structure other than proportion of snags in the overstory. Marten numbers were negatively correlated with an increase in snags, because areas containing mountain pine beetle infestations were selected by the Forest Service for salvage logging, and therefore contained more clearcuts than areas that were not infested.

Introduction

Studies of American martens (*Martes americana*) in extensively clearcut forests suggest that martens may be sensitive to certain levels of forest fragmentation (Soutiere 1979, Snyder and Bissonette 1987, Thompson and Harestad 1994). However, marten population responses to gradual increases in fragmentation are not well known. Marten populations might exhibit a linear negative response to increased fragmentation, since martens generally avoid clearcuts and other large openings, especially in the winter (Clark and Campbell 1979, Soutiere 1979, Steventon and Major 1982, Hargis and McCullough 1984). However, aspects of marten foraging ecology suggest that marten density could increase at low levels of fragmentation, because martens forage in clearcuts during summer (Soutiere 1979), and hunt along forest edges (Simon 1980, Spencer et al. 1983). Moreover, diets of martens are not restricted to forest-associated prey (Weckwerth and Hawley 1962, Koehler and Hornocker 1977, Buskirk and MacDonald 1984). If martens prey on species associated with clearcut edges as well as forests, then low levels of fragmentation might improve habitat quality by increasing the abundance and diversity of prey. However, a decline in marten populations would eventually occur as additional clearcuts caused forested habitat to become limiting. This result could be manifest as either a gradual decline in marten density, or as a threshold response associated with a critical ratio of forest to clearcuts. A threshold response might be expected when forest cover no longer spanned a landscape as 1 connected patch, requiring martens to cross openings to reach forest patches.

We studied a series of clearcut landscapes to investigate responses of marten populations to gradual increases in fragmentation caused by timber clearcuts. Our primary objective was to determine whether sensitivity of martens to fragmentation was linear, or whether there were specific levels of fragmentation associated with either an increase in habitat quality or a critical threshold of decline. Our secondary objective was to compare small mammal abundance among forests, meadows, and clearcuts to determine how forest fragmentation affects the availability of potential prey.

Study Area

We selected 18 sites in the Uinta Mountains of northern Utah to represent various levels of forest fragmentation caused by clearcutting. The sites were at 2700-3200 m elevation and were predominantly vegetated with mature forests of Engelmann spruce (*Picea engelmannii*) and lodgepole pine (*Pinus contorta*), with occasional subalpine fir (*Abies lasiocarpa*). Each site served as a sampling unit delineated by a square area of 9 km^2. We selected sites that were as similar as possible in terms of stand structural characteristics representing suitable habitat for marten, including canopy cover >30%, large trees, and abundant, coarse woody debris. The sites differed primarily in the amount of timber harvesting that had taken place, ranging from completely unharvested to 42% cut. Many sites also contained natural fragmentation from meadows and boulder fields, which covered 2%-12% of the area. Total fragmentation from both clearcutting and natural openings ranged from 2%-42% (Table 1).

We selected sites in which the majority of clearcuts were at least 5 years old to increase the likelihood of a stable marten population relative to the landscape pattern. However, this choice was not always possible, and 1 site, Marsh West, was characterized by clearcuts <2 years old, whereas 2 other sites, Manila and Long Park, contained clearcuts that had been harvested the previous year. However, new harvest blocks within these latter sites represented <3% of total clearcuts within each landscape.

Average ($\bar{x} \pm$ SD) clearcut size was 10 ± 6.4 ha. The majority of clearcuts were sparsely vegetated and provided a distinct seral contrast with adjacent forests. Vegetation was predominantly grasses, sedges, and forbs, with conifer tree heights generally <2 m and no forest canopy cover. Clearcuts lacked coarse woody debris, because logging slash was routinely piled and burned immediately after harvest.

Methods

Fragmentation Analysis

We developed raster images of our study sites using ERDAS, a geographic information system. Our sites were each 101 × 101 pixels in extent and were extracted from a vegetation map of Utah developed for a species-distribution gap analysis (Edwards et al. 1995). The original map was based on thematic mapper data with 30-m resolution, and was classified into 35 vegetation types. We aggregated the vegetation types into 3 habitat categories: forests, natural openings, and clearcuts.

We also simplified the maps to reflect the scale at which martens appear to perceive their habitat. Assuming that martens would cross 30-m openings

Table 1. Habitat-type percentages in 18 landscapes (each 9 km^2) in the Uinta Mountains of northern Utah.

Site	Mature forest (%)	Natural openings (%)	Clearcuts (%)
Beaver	98.3	1.7	0.0
Anderson	95.4	1.2	3.4
Highline	94.2	2.9	2.9
Spirit	92.4	7.6	0.0
Sims	91.7	3.3	5.0
Marsh East	90.9	0.2	8.9
Bull	90.1	9.9	0.0
Manila	85.8	4.3	9.9
Sheep	85.7	3.1	11.2
Cliff	84.4	12.3	3.3
Chepeta	83.3	4.6	12.1
Hayden	83.2	6.3	10.5
Dahlgreen	80.5	1.1	18.4
Deer	78.4	6.4	15.2
Marsh West	74.7	5.7	19.6
Long Park	63.9	4.9	31.2
Gold	60.9	30.3	8.8
East Park	58.1	0.0	41.9

(Koehler and Hornocker 1977, Hargis and McCullough 1984), we reclassified isolated non-forested pixels and strips of non-forested habitat 1 pixel (30 m) wide as forest. Likewise, isolated forest pixels embedded in an open polygon were reclassified to match the habitat category of the polygon.

Natural openings were combined with clearcuts in the analysis of fragmentation patterns. We calculated the proportion of each landscape occupied by unforested areas as our primary measure of forest fragmentation.

Estimates of Marten Density

We estimated relative marten densities within each site through summer live-trapping. Twenty-five live-traps were placed in a systematic grid within each site and monitored for 6 consecutive nights, yielding a total effort of 150 trap-nights

per site. We sampled each site at least once during 4 trapping periods between 1991-1993. We resurveyed 9 sites over 2 years to examine potential differences in capture rates between years, and 1 site was surveyed all 3 summers to estimate the magnitude of change in capture rates over the entire span of the study. To examine potential differences in capture rates from early to late summer, we resurveyed 4 sites twice during early and late summer of the 1992 season.

Captured martens were sedated, weighed, and ear-tagged. We determined the gender and reproductive status of each individual and estimated age as either adult or juvenile based on the development and wear of teeth.

We used the number of individual martens captured within each site per trapping effort as the primary measure of the response of martens to increasing fragmentation. However, because density is not always correlated with habitat quality (van Horne 1983, Pulliam 1988), we used reproductive activity, body weights and condition, and overwinter success, as other evidence to augment information on marten density.

Estimates of Prey Abundance

We surveyed small mammal populations within each site in order to differentiate the effects of prey abundance from those of fragmentation. We conducted a snap-trap survey between 22 July and 8 September 1992, using 12 lines of snap traps within each site. Each trap line consisted of 50 traps set out in 16 stations of 2 mouse traps and 1 rat trap per station, except for the final station, which consisted of 1 mouse and 1 rat trap. Stations were spaced 20 m apart. The lines were placed in forested areas, clearcuts, and meadows in proportion to the availability of each of the 3 habitat types, and were run for 2 nights, yielding 1200 trap nights per study site. Actual trap nights were calculated by subtracting all traps that malfunctioned or were sprung each night. We monitored 6 lines at a time and spent 4 consecutive nights at each site.

Traps were checked in early morning and late afternoon to maximize captures of both diurnal and nocturnal species, and to minimize loss of captures to scavengers. However, sprung traps were not reset between morning and afternoon checks, and the 2 periods were considered 1 trapping effort. We recorded species, weight, and gender of each animal captured, estimated the age as either juvenile or adult, and noted the reproductive status of females. We estimated the relative abundance of each species using captures per 100 trap-nights, and calculated total biomass based on measured weights. The data were summarized by site and by habitat types within each site.

Forest Structure

Although we selected sites in mature forests to minimize differences in forest habitat among sites, measurements of structural attributes were required to verify

site similarity and to test for marten population responses to any structural attributes that might differ. Data were obtained from a modified plotless cruise at 25 points within each study site. The points were located at random compass directions and random distances between 1 and 30 m from each marten trap. At each point, we used a basal area prism to determine the number of trees included within the variable plot, and for each tree we recorded the height, diameter (dbh), species, crown class, live crown ratio, and snag decay class.

We estimated the amount of conifer reproduction by tallying all trees <7 cm dbh within 2-m radius plots located 5 paces from each sampling point in the 4 cardinal directions. Canopy cover was calculated with a densiometer at the center of these 4 plots.

We determined the abundance of coarse woody debris using the inventory procedure developed by Brown (1974). We established 2 15-m transect lines that extended from the plotless cruise sampling point in random directions, and recorded the diameter at intersection of all woody material >10 cm encountered along the lines. We classified the logs as being either sound or rotten. Coarse woody debris data were summarized as kg/ha for sound and rotten decay classes, using the calculations developed by Brown (1974).

Statistical Analyses

Each site was surveyed 1-3 times out of 4 sampling periods. We used a bootstrap technique (Efron and Tibshirani 1993) to randomly generate 35 unique combinations of marten captures from the 4 periods, selecting 1 sampling period from each site. These combinations were used to form 35 data sets (n = 18 per data set) consisting of individual marten captures and total trap-nights associated with each site and sampling period. The survey was designed to yield 150 trap nights per site, but actual trap nights varied among sites due to field conditions.

We used Poisson regression analysis (Frome et al. 1973) to test for differences in marten capture rates among sites as a function of fragmentation, prey abundance, and forest structure. We chose the Poisson model because marten captures were counts that occurred at a low rate, and the data most closely fit the Poisson distribution. For prey abundance and forest structure, we explored 7 prey and 33 forest structure variables and selected 1 prey and 1 forest structure variable having the highest correlation with marten captures for incorporation into the model.

The response variable in the model was individual marten captures per 100 trap-nights, expressed logarithmically in a Poisson regression as *ln* (captures/100 trap-nights). The 2 components of the term are factored into *ln* (captures) - *ln* (100 trap-nights), with captures used as the primary response measure and 100 trap-nights used as an offset term in the regression model (McCullagh and Nelder 1991).

Model parameters were estimated using maximum likelihood estimation (Kendall and Stuart 1946, Kleinbaum et al. 1988). We compared the full model containing all 3 explanatory variables to a set of reduced models in which 1 of the 3 parameters was dropped. The criterion for a good fit was based on the change in model deviance between the full and reduced models, which is analogous to comparing regression sums of squares in linear regression analysis. Because the change in deviance between the full and reduced models follows a chi-square distribution (Frome et al. 1973), we used a chi-square statistic to report the significance of each model parameter.

Small mammal survey data were summarized by 7 variables: total biomass of all prey, captures/100 trap nights of all prey, and captures/100 trap nights of the 5 most frequently trapped species. To reduce unnecessary forest structure descriptors from the original 33 variables, we compared box and whisker plots for each variable across all sites and eliminated variables that showed only marginal differences among sites. Ten variables exhibited sufficient differences to warrant further analysis: basal area (m^2/ha) of live overstory trees; average quadratic mean diameter (dbh_q) (cm) of overstory trees, of overstory spruce, and of overstory lodgepole pine; percent of live overstory in spruce and in lodgepole pine; and the abundance of snags, expressed in 4 variables: the percent of total stems, percent of overstory stems, total basal area, and live overstory basal area. We entered all 7 prey variables and 10 forest structure variables into a forward stepwise regression along with the percent of the landscape unforested, and chose the first prey and forest structure variables entered into the regression model for incorporation into our final model.

Results

Marten Captures

Individual marten captures per trapping period ranged from 0-8 per site. Between 1991-1993, we captured 53 individuals (34 males and 19 females) in 4893 trap nights. For sites resampled during 2-3 trapping periods, we found no significant difference in capture rates among trapping periods ($\chi^2 = 2.89$, df = 3, $P = 0.41$). Sites with high captures were consistently high, and sites with 0 captures remained low (Table 2). This consistency resulted in a fairly stable ranking of sites across years, indicating that the differences in captures were due to factors other than seasonal variation or sampling error.

Several population attributes confirmed that high marten densities indicated high quality habitat. The 2 sites with the highest captures were the only sites where we observed overwinter success, based on captures in subsequent years. These sites also represented 2 of 4 sites with lactating females, denoting reproductive activity. Although we found no correlation between mean adult male

Table 2. Individual marten captures within 9-km^2 sites in the Uinta Mountains of northern Utah.

Site	1991	1992a[1]	1992b[2]	1993
Hayden	7		4	8
Highline	4		3	
Beaver				3
Bull	3			
Dahlgreen				3
Deer		2	2	0
Spirit	1		3	
Anderson	2			
Sims		1	2	
Chepeta	1		1	
Cliff			1	
Sheep				1
Long Park	1		0	
Manila		0	0	0
Marsh East	0	0		
Marsh West		0	0	
Gold		0		0
East Park				0

[1] Sampling period June 10 to July 15, 1992.

[2] Sampling period July 19 to Sept. 10, 1992.

Blanks represent sampling periods during which trapping did not occur at that site.

body weights and marten densities ($F = 0.332$, df = 9, $P = 0.58$), the average weight of males at the site with the highest captures was greater than the average for all sites. Overall body condition was fair to excellent in sites with high densities. We found poor body condition in 2 sites with only 1 marten capture: 1 site yielded a blind male and another, an emaciated, lactating female.

Marten Response to Fragmentation

Individual marten captures were negatively correlated with fragmentation and snag abundance (Fig. 1). Only 1 marten was captured in over 900 trap-nights within 4 sites that were more than 25% unforested, and this capture occurred in the least fragmented portion of a site (Fig. 2). Three of these sites were surveyed twice to ensure that low captures were consistently obtained.

The full model included percent of landscape unforested, vole captures per 100 trap-nights, and percent of the overstory in snags, with the latter 2 variables

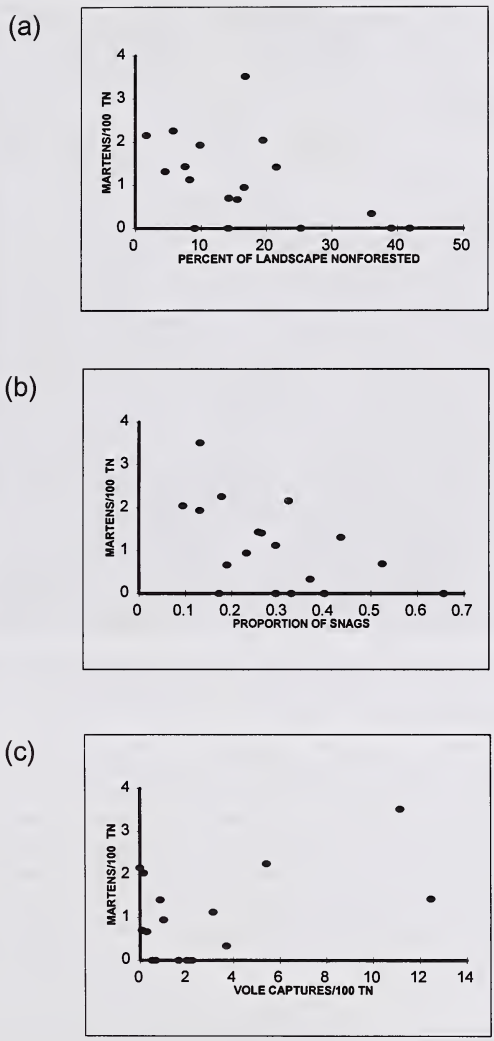

Figure 1. Correlations of marten captures per 100 trap-nights (TN) with (a) fragmentation, (b) snag abundance, and (c) vole density.

Figure 2. A 30%-unforested site (Long Park) in the Uinta Mountains of northern Utah. The sole capture of a marten was in the least fragmented, southwest quarter of the image.

representing the best correlates with individual marten capture rates of all prey and forest structure variables examined. When all 3 variables were included in the model, vole captures per 100 trap-nights did not contribute significantly (mean $P = 0.53$, CI = 0.50, 0.56) to the model and was therefore dropped from the analysis. In the reduced model, percent of each landscape unforested and percent of the overstory in snags were both significant (percent of each site unforested: mean $P = 0.03$, CI = 0.02, 0.04; percent of the overstory in snags: mean $P = 0.01$, CI = 0.01, 0.01).

Prey Abundance

Density of small mammals, based on captures/100 trap-nights, was highest in clearcuts, followed by forests and meadows (Wald χ^2 for clearcuts *versus* forests = 20.12, df = 1, $P = 0.001$; Wald χ^2 for meadows *versus* forests and clearcuts = 16.14, df = 1, $P = 0.001$) (Table 3). We captured an average of 21 mammals/100

Table 3. Captures per 100 trap-nights of the 5 most commonly trapped species in a survey conducted during the late summer of 1993 within 18 sites in the Uinta Mountains of northern Utah.

Species	Forests	Meadows	Clearcuts
Southern red-backed vole	5.3	0.4	0.9
Deer mouse	4.9	3.8	14.4
Uinta chipmunk	1.7	0.2	1.8
Least chipmunk	0.2	0.0	2.6
Vagrant shrew	0.1	0.0	0.1
Total mammals[a]	14.0	6.4	21.5

[a] Includes other less commonly trapped species.

trap-nights in clearcuts, 14/100 trap-nights in forests, and 6/100 trap-nights in meadows. Total biomass of all mammals captured, excluding snowshoe hare (*Lepus americanus*), was highest in clearcuts, followed by forests and meadows ($F = 17.5$, df = 2, $P < 0.001$).

The 5 most commonly trapped species were southern red-backed vole (*Clethrionomys gapperi)*, deer mouse (*Peromyscus maniculatus*), Uinta chipmunk (*Tamias umbrinus*), least chipmunk (*Tamias minimus*), and vagrant shrew (*Sorex vagrans*) (Table 3). Red-backed vole densities were highest in forests (Wald $\chi^2 = 23.3$, df = 2, $P < 0.001$), with mean capture rates of 5/100 trap-nights, and deer mouse densities were highest in clearcuts (Wald $\chi^2 = 66.5$, df = 2, $P = 0.0001$), with mean capture rates of 14/100 trap-nights. Least chipmunk captures were predominantly in clearcuts (Wald $\chi^2 = 46.6$, df = 2, $P < 0.001$), but Uinta chipmunk captures occurred in both clearcuts and forests at nearly equal rates (Wald $\chi^2 = 0.08$, df = 1, $P = 0.78$).

Individual marten captures were not significantly correlated with any small mammal species. The only apparent correlation was a positive association between marten captures and southern red-backed voles, but further analysis revealed that the apparently strong relationship was due to high leverage from 1 site, Hayden, which had the highest marten capture rate and the second highest density of voles (Fig. 1). Whereas most sites yielded 2-4 vole captures per 100 trap-nights, Hayden produced 11 captures per 100 trap-nights. When this site was removed from the analysis, the correlation between marten captures and vole densities was not significant.

Discussion

Marten density declined with increasing fragmentation as measured by the percent of the landscape unforested. This decline appeared to be roughly linear,

although the graphed relationship indicated a possible step function with a threshold near 25% (Fig. 1). This apparent threshold should not be overinterpreted because each level of fragmentation was represented by only 1 site; however, the suggestion of a threshold provides a basis for the focus of future research.

Regardless of the exact nature of the correlation, the marten density response to fragmentation is clearly negative, and provides no evidence that marten density might increase at low levels of fragmentation due to an increase in abundance or diversity of potential prey associated with clearcuts. Marten density was not positively correlated with any species found in clearcuts. The highest number of individual marten captures was in a site having high densities of the southern red-backed vole (Fig. 1), a forest-associated species (Raphael 1989, this study). Our data on prey abundance are incomplete because we were unable to acquire information on the abundance of snowshoe hare (*Lepus americanus*) and red squirrel (*Tamiasciurus hudsonicus*) with the snap-trap survey method; both of these species are potential prey of martens (Hargis and McCullough 1984).

Marten capture rates reached 0 at remarkably low levels of fragmentation. Landscapes with 25%-42% of the area unforested each contained a connected forest matrix, allowing potential movement by martens throughout most of the forest without having to cross an opening (e.g., Fig. 2), yet martens were apparently not using these sites or were using them at densities lower than we were capable of detecting with repeated surveys. Sites with 0 captures may represent a true loss of martens from the area, or they may represent densities so low that our trapping efforts did not register marten presence.

The lack of marten captures in sites >25% unforested indicates greater sensitivity to fragmentation than has been reported elsewhere. Snyder and Bissonette (1987) reported marten captures in residual forest patches <24 ha in size that were isolated from larger patches of uncut forest, although the capture rates were substantially lower than in uncut landscapes. Soutiere (1979) found marten using areas that were 60% cut in Maine, although at lower population levels than in uncut areas. The clearcuts in our sites may be more inhospitable to marten than those in Maine because they lack deciduous vegetation reportedly used as cover by marten in summer months (Soutiere 1979, Steventon and Major 1982).

We observed a decline in marten captures with an increasing proportion of snags in the overstory. Some sites were infested with mountain pine beetle (*Dendroctonus ponderosae*) resulting in highly variable snag proportions, ranging from 0.09 for an uninfested site to 0.65 in a site where most of the landscape was infested. The proportion of snags in the overstory was positively correlated with the percent of each landscape in clearcuts ($F = 6.54$, df = 1, $P = 0.02$) because timber harvests are often placed in stands infested with mountain pine beetle to salvage the wood. Therefore, the negative correlation between marten density and snags echoed the relationship between marten density and fragmentation from clearcutting.

In contrast to our findings, marten use of snag-dominated stands was high in Newfoundland (Drew 1995). Newfoundland is a large island with low faunal diversity and does not possess a forest-associated vole. The principal prey for marten in Newfoundland is the meadow vole (*Microtus pennsylvanicus*), which is more abundant in forests with open canopies than closed-canopy stands (Sturtevant and Bissonette, this volume). Thus, snag-dominated stands in that environment provide suitable conditions for this species. In the Uinta Mountains, we found no correlation between vole densities and snag abundance ($F = 1.29$, df = 1, $P = 0.27$), and the avoidance of areas with high proportions of snags was associated with landscape pattern rather than ecological conditions within the stands.

Management Recommendations

Current management recommendations for the American marten tend to focus on attributes used by martens at finer scales, such as coarse woody debris and characteristics of stand structure. However, forests with the required structural attributes may be unsuitable for marten if they occur in highly fragmented landscapes. It has been assumed that martens will use small forest patches if these are connected by forested corridors, but our study suggests that landscapes with as little as 25% unforested habitat may be unsuitable for martens, especially if open areas provide insufficient structure and vegetation for marten use in summer months. Because our study was limited to high elevation forests in Utah where the contrast between forest and openings was high, it is difficult to determine whether marten populations would show a similar response to 25% unforested habitats elsewhere. The key to differences in marten population response may lie with the time required for harvested areas to develop vegetative structure, and we anticipate similar responses of martens in areas where open areas are poorly vegetated for long periods.

Until further study can be undertaken in other geographic areas, we recommend a conservative approach be taken toward landscape pattern. Areas managed for viable populations of marten should not only contain the requisite forest structure, but have <25% of the total management area committed to unforested habitats. The proportion of total area occupied by natural openings should be included in this calculation. Efforts should be made to aggregate clearcut blocks so that larger areas of undisturbed forest can be maintained.

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SHORT-TERM EFFECTS OF CLEARCUTTING ON MARTENS AND THEIR PREY IN THE BOREAL FOREST OF WESTERN QUEBEC

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Abstract: From August 1990 to October 1994, we studied movements and survival of American martens (*Martes americana*) in 3 forest blocks, Rapide 7 East (R7E, 70 km²), Rapide 7 West (R7W, 91 km²) and Kinojévis (KINO, 123 km²), in western Québec. About 60% of the KINO block was logged during our study by the cutting method with protection of regeneration (CPR), a clearcutting technique using equally spaced skidding trails to protect advanced regeneration. We obtained 159 captures of 95 martens with a trapping effort of >7500 trap-nights. Trapping success was much higher in R7E (5.5-6.4 martens/100 trap-nights) than in R7W (1.2-1.3). Although trapping success was moderate (1.4 martens/100 trap-nights) in KINO 1 or 2 years after logging, it is probable that marten density decreased following clearcutting. Annual home ranges of males (95% minimum convex polygon, $\bar{x} = 7.7 \pm 0.8$ [SE] km², $n = 26$) were not different between R7 and KINO blocks ($P = 0.37$), but martens in KINO using clearcut areas had home ranges almost twice as large as those living in uncut portions of that block ($P = 0.040$-0.055). Minimum distances travelled per 24 h by males were greater in KINO than in R7 (1470 ± 60 *versus* 1240 ± 90 m, $P = 0.022$). Annual dispersal rates (0.32 ± 0.12 *versus* 0.16 ± 0.08 per year, $P < 0.01$) and natural mortality rates of males (0.38 ± 0.12 *versus* 0.31 ± 0.10 per year, $P < 0.01$) were higher in KINO than in R7. Relative abundances of small mammals and snowshoe hares (*Lepus americanus*) were estimated before and after clearcutting in 5 treated and 5 control stands in R7. Red-backed vole (*Clethrionomys gapperi*) was the predominant small mammal species in both stand types before logging (5.5-6.0 captures/grid) but reached a lower level in the treated stands immediately after logging (69% pre-logging level in treated stands *versus* 131% in controls, $P = 0.04$). Conversely, captures of deer mice (*Peromyscus maniculatus*) increased in treated grids after cutting, but not in controls (4.6 ± 0.6 *versus* 1.5 ± 0.4 captures/grid, $P < 0.02$). Numbers of hare decreased in treated stands after logging (0.2-0.7 *versus* 5.3-9.9 pellets/plot, $P < 0.01$). We conclude that large clearcuts in boreal forest, even with the CPR technique, reduced the density of martens, but that marten appear more tolerant to forest fragmentation than was previously reported.

Introduction

The American marten (*Martes americana*) is used as an indicator species of the "well-being" of forests (Bull et al. 1992, Buskirk 1992). The marten is a fur-bearer that occurs at its highest density in mature stands (Thompson 1988). It is sensitive to disturbance because it has small fat reserves (Buskirk and Harlow 1989) and therefore seems to be constantly hunting for prey (Thompson 1986). Furthermore, it needs large areas to establish its home range: Buskirk and McDonald (1989) have estimated that marten spatial requirements are 3 times greater than the average carnivore, based on the relationship between body mass and home-range size (Lindstedt et al. 1986). Thompson (1991) promoted the marten as a symbol for the preservation of old-growth forest in eastern North America, much like the spotted owl (*Strix occidentalis*) is used in the western United States (Bart and Forsman 1992). The marten is generally associated with coniferous forests that have a complex structure, often with old uneven-aged stands (Buskirk 1992). Data for eastern North America indicate similar relationships (Thompson 1988, 1991; Bissonette et al. 1989; Thompson and Harestad 1994).

Martens are severely affected by clearcuts. Studies reviewed by Thompson (1988) and Thompson and Harestad (1994) showed that marten densities remained low up to 40 years after clearcutting. In Newfoundland, marten densities were much lower in cutover areas up to 23 years old compared to densities in uncut areas, but marten inhabited larger residual forest patches in the clearcuts (Snyder and Bissonette 1987; Bissonette et al. 1988, 1989). In Maine, cutovers about 15 years old had low marten densities whereas partially cut areas had densities similar to uncut forests (Major 1979, Soutiere 1979, Steventon and Major 1982). In Ontario boreal forests, logged areas <40-years-old are a suboptimal habitat for marten compared to old-growth stands (Thompson 1986, 1994; Thompson and Colgan 1987, 1990, 1994; Thompson et al. 1989).

Forest management prescriptions to maintain marten habitat generally involve setting aside large reserves of mature forest. Soutiere (1979) suggested leaving 25% of the area as uncut blocks. Bissonette et al. (1988, 1989) proposed a landscape approach with cutovers less than 500 m wide interspersed in an old-forest matrix. When clearcutting is applied, Lofroth and Steventon (1990) recommended leaving 50% of the area uncut. Thompson and Harestad (1994) suggested that, within 5000-km^2 landscapes, 20% of the area be kept as mature forest. To maintain marten populations, Naylor et al. (1994) proposed >5-km^2 leave blocks of optimal and suitable habitat no more than 5 km apart and interconnected with a network of corridors.

Clearcutting is the usual harvest method in the boreal forest. More than 90% of the wood harvested in Canada is logged by this technique (Gingras 1993). The potential impact on the environment, and marten species in particular, is great.

Jurisdictions have adopted constraint management rules to minimize negative impacts (Dodds 1994). For example, since 1988 in Quebec, cutovers cannot exceed 250 ha and must be separated by leave strips 60-100 m wide; 20-m riparian buffer strips are retained along lakes and each side of permanent streams; uncut forest blocks 3-10 ha in size and comprising 4% of the area must be dispersed throughout cutovers (MER 1989). New forest-harvesting standards were adopted in 1996. Typically, a landscape logged by the 1988 standards would contain 10-15% of the area as reserves, much less than the 20-50% in uncut forest that is recommended to maintain marten habitat.

Silvicultural systems, including yarding methods, have evolved in recent years. In Quebec, advance regeneration is usually abundant in coniferous stands and the cutting method with protection of regeneration (CPR) is gradually replacing traditional yarding methods (Fig. 1). About half of the cutovers in Quebec were done by the CPR method in 1991 (M. Tremblay, Que. Minist. Ressour. Nat., pers. commun.); this proportion has increased substantially since 1991. The CPR method involves less disturbance to the site because the logging machinery is confined to equally spaced trails (Gingras 1993, Richardson 1993). Shrubs and smaller trees between trails are undisturbed, hence the cutovers retain a substantial proportion of ground and shrub cover. Because advance regenera-

Figure 1. Aerial view of an area clearcut by the cutting method with protection of regeneration (CPR). This method involves less disturbance to the site because logging machinery is confined to equally spaced trails.

tion is retained, cut blocks logged by the CPR method succeed to coniferous forest more rapidly than do cut blocks logged by other yarding methods.

Although the effects of clearcutting on marten have been previously studied, the current cutting practices need reevaluation because the yarding methods used (CPR) and the resulting pattern of cut blocks across the landscape are different. We studied marten over a 4-year period in 3 large forest blocks, 2 control areas and a recently harvested area. The objective of our study was to measure the short-term effects of the CPR technique on martens and their prey, as applied following the constraint management rules prevailing in Québec from 1988 to 1995. We hypothesized that (1) marten density and survival would be lower in the treated block, (2) martens frequenting cutovers would have larger home ranges and make longer movements, and (3) prey abundance would decrease after cutting.

Study Area

Movements and survival of martens were studied in 3 blocks south of Rouyn-Noranda and Val-d'Or, western Québec: from August 1990 to summer 1992 in Rapide 7 East (R7E, 70 km², 47°41'N, 78°16'W) and Rapide 7 West (R7W, 91 km², 47°41'N, 78°30'W), and from summer 1992 to October 1994 in Kinojévis (KINO, 123 km², 48°00'N, 78°50'W). The climate in all areas is continental with winter temperatures often below -30°C at night. Black spruce (*Picea mariana*), jackpine (*Pinus banksiana*), balsam fir (*Abies balsamea*), and white birch (*Betula papyrifera*) are the dominant tree species. In 1990, only 2% of R7E and 10% of R7W had been clearcut during the last 20 years. No cutting was done in these blocks during the marten study but logging occurred from summer 1992 to fall 1994. Blocks R7E and R7W are referred to as our controls for marten (no cutting). From 1990 to 1994, 39% of KINO was harvested with the CPR technique. If we include all fragmented patches created by logging (leave and buffer strips, uncut blocks, immature stands dispersed in clearcuts), the size of the area over which logging occurred was 74 km², or 60% of the KINO study area. The landscape of the treated block is a cutover matrix occupying the core surrounded by contiguous forest (Fig. 2). In this matrix, the residual forest is fragmented and composed of narrow corridors 40-100 m wide along streams or between cutovers, and small patches of uncut forest reserves or non-commercial young stands.

Trapping is allowed in the 3 blocks. R7E is part of a "beaver (*Castor canadensis*) preserve" accessible only to Native people. Although we have no precise data, trapping pressure is probably lower there than in R7W, which is divided into traplines. In KINO, the trapper occupying the sole trapline agreed to not trap marten during our study.

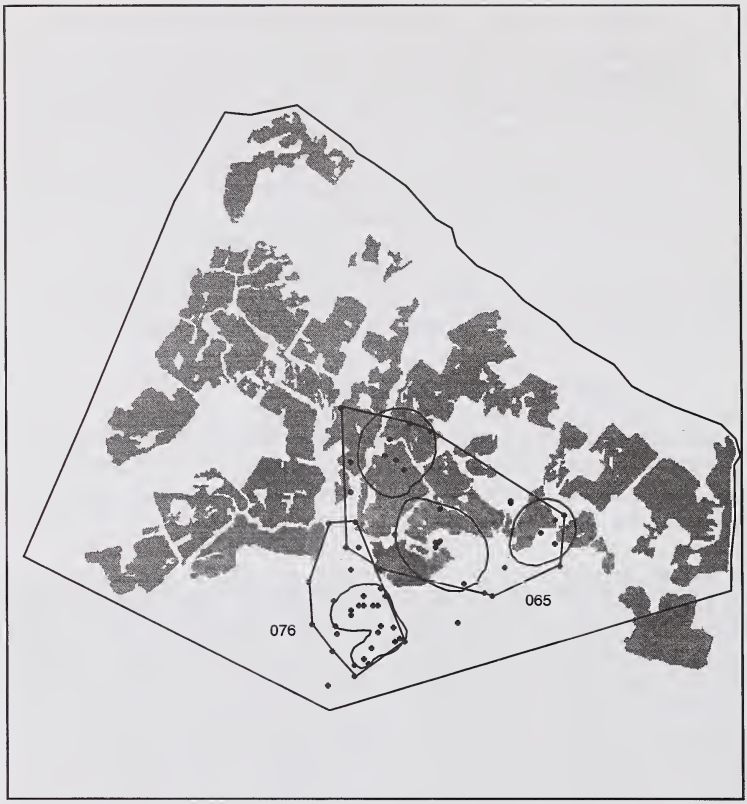

Figure 2. Landscape of the Kinojévis block (KINO), composed of a cutover matrix core surrounded by contiguous forest. Telemetry locations, 95% minimum convex polygons, and 60% kernels of 2 martens are illustrated: marten 065 has 3 kernels and frequents clearcut areas; marten 076 has 1 kernel and lives in uncut portions of the block.

Numbers of snowshoe hare (*Lepus americanus*) and small mammals were measured in 10 forest stands (about 20 ha each) in R7. These stands were selected from forest maps in 1990, 5 as controls and 5 in areas where logging was planned (treated stands). These treated stands were cut during summer 1992.

Methods

Martens were trapped in collapsible Tomahawk 202 traps (15 × 15 × 48 cm) set in coniferous and mixed stands accessible along forest roads or water bodies. Captured martens were anaesthetised with 3 cc of isofluorane injected into a plexiglass box containing the trap. They were sexed and weighed, and an upper first premolar was usually extracted to determine age class (Strickland et al. 1982). In R7, martens were fitted with a Lotek SMRC-5 radio-collar weighing 40-42 g. In KINO, females received 31-g and males 38-40-g Holohil collars. A numbered metal tag was attached to the right ear of each animal.

We located radio-collared animals from a Bell 206B helicopter (88% of locations) or a Cessna 185 airplane (12%), using the technique described by Gilmer et al. (1981). Telemetry locations were done 1-2 times per month except during winters 1991-1992 to 1993-1994, when we made 10-15 daily locations in January and March, or during the last year (1994), when some animals were located twice per day. Locations were plotted on topographic maps at a scale of 1:50,000 (R7) or 1:20,000 (KINO) and UTM coordinates were determined to the nearest 100 m or 20 m, respectively.

Telemetry locations were scrutinized before analysis. Locations of each animal were plotted and extreme or unusual data were verified to eliminate erroneous ones. Some animals made large movements outside their usual home range immediately after collaring. These locations were discarded because they were likely the result of our interference. Martens were classified as dispersers, residents, or unknown. Dispersing animals usually moved with no definite pattern of home-range fidelity and were eventually located >10 km from the block boundary. Resident animals had a stable home range. Unknowns were not followed long enough to establish their status. We considered 3 age groups, juveniles (<1 year old), adults, and unknowns.

Home ranges were computed with CALHOME software (Kie et al. 1994) for 2 periods, the entire year and the winter season (1 December to 31 March). Many algorithms are available to obtain home ranges. We selected the minimum convex polygon (100% and 95% locations) and the adaptative kernel. The minimum convex polygon technique is more widely used (Harris et al. 1990), so that its results can be compared with most other studies (e.g., Buskirk and McDonald 1989). The adaptative kernel (Worton 1989) enables a description of the intensity of utilization and is considered a better technique than the harmonic mean (Worton 1987, Kie et al. 1994). The kernel computes probability areas containing predetermined proportions of the locations. To establish the acceptable sample size, the usual procedure is to plot a curve describing the surface area of the home range and the number of locations (Laundré and Keller 1984, Harris et al. 1990). We conducted a pre-test on 15 animals by randomly selecting a set of

locations (n = 3, 6, 9, 12, 15, 20, etc.) and computing the corresponding area of 2 minimum convex polygons (100%, 95%) and 4 kernels (95%, 75%, 60%, 50%). For animals having fewer observations than the acceptable sample size suggested by the pre-test, we plotted a curve of the cumulative surface area as new locations were obtained by telemetry, to verify that an asymptote was reached.

Observations are independent if location at time t is not related to location at time t-1, a prerequisite for most home-range techniques (Worton 1987). To check independence, we computed Schoener's ratio described by Swihart and Slade (1985), which is based on the distance between locations at time t and t-1, and distance to the center of activity. As suggested by Swihart and Slade (1986), to minimize Type II errors, we used a ratio exceeding $P > 0.25$ to declare independence of telemetry observations. A simpler test, examining if distances between successive locations are related to the time interval (Arthur et al. 1989), was also performed.

For resident marten, we computed the minimum distance per 24 h, which is the linear distance between 2 successive locations separated by a 1-day interval. Mortality rates were estimated with MICROMORT software (Heisey and Fuller 1985), using 3 time intervals (spring-summer, 1 April to 31 August; fall, 1 September to 30 November; winter, 1 December to 31 March) and 2 causes of death (trapping, other causes). Survival period for each animal was defined as the number of days from collaring to the last telemetry location. Mortalities and survival days that occurred after radio contact had been lost were not considered. They would have biased estimates because such data were not available for surviving animals. Dispersal rates were computed with MICROMORT, by assuming that animals that had left the study blocks were "alive" until their dispersal and that they "died" when leaving.

Numbers of snowshoe hare were estimated from 1991 to 1994 by counting fecal pellets in permanent plots established in August 1990 in 5 control and 5 treated stands (Litvaitis et al. 1985). Circular, 1-m radius plots were systematically spaced each 20 m along 2 adjacent transects 100 m apart per stand, with 15 plots per transect. Pellets were counted and cleared from the plots annually in May.

Small mammals were live-trapped each year from 1990 to 1994 between mid-August and mid-September in $7.6 \times 9 \times 23$ cm Sherman collapsible traps (Davis 1982). Two trapping grids were placed in the same stands used for the hare survey. Each grid contained 4×10 points spaced 10 m apart, with 2 traps at each point. Traps were set during 4 consecutive 24-h periods. After capture, small mammals were marked by toe clipping or ear tagging and then released. The total number of different individuals per grid for each species was used as an index of relative abundance.

Statistical analyses were done with SPSS/PC 4.1 software (Norusis 1990). Normality distribution and homogeneity of variances of variables were examined and appropriate transformations performed before using parametric tests. A 1-way ANOVA, followed by a Scheffe multiple range test when >2 means were involved, was used to compare home-range size (square root transformation) and minimum distance per 24 h ($\sqrt{x+1}$). Mortality and dispersal rates were tested with the *Z* statistic (Heisey and Fuller 1985). Repeated measures ANOVA was used for the number of hare pellets (*ln* x+1) in 1991-1992 and captures of red-backed vole (*Clethrionomys gapperi*) (*ln* x+1). Numbers of hare pellets in 1993-1994 and captures of deer mice (*Peromyscus maniculatus*) were compared before and after logging using a nonparametric Mann-Whitney *U*-test because the data could not be normalized.

Results

We obtained 159 captures of 95 martens (56 males, 38 females, 1 unknown), 57 in the R7 blocks and 38 in KINO block, with a trapping effort of >7500 trap-nights. Based on fall captures, the sex ratio (167 *versus* 164 males/100 females) and the proportion of juveniles (65% *versus* 54%) were not different between blocks (χ^2 test, $P > 0.10$). Average body weights were similar ($P > 0.73$) between blocks: males were 934 ± 28 g ($n = 38$) in R7 and 942 ± 93 g ($n = 29$) in KINO; females were 636 ± 18 g ($n = 23$) in R7 and 626 ± 16 g ($n = 17$) in KINO. Because each block was trapped by the same crews and with the same technique, we used trapping success of marten as an index of density (Table 1). Trapping success was moderate in KINO (1.4 martens/100 trap-nights) and in R7W (1.2-1.3), but much higher in R7E (5.5-6.4). It remained similar over the 2 consecutive years of study in each block. Seven animals were not radio-collared because they either died in the live-trap or during manipulation (5), or were too small (2).

A total of 1557 locations was obtained from 88 collared animals (55 in R7, 33 in KINO). Because of early loss of radio-contact (9 in R7, 2 in KINO), mortality (19, 7), collar loss (1, 0) or dispersal (4, 3), only 43 martens (22, 21) provided locations over a period of 90 days or more. Of those martens, 35 (16, 19) had 9 locations or more and were used for the home-range analyses. Nine animals (4, 5) were followed for more than 500 days.

Based on Schoener's ratio, locations of fewer than half of the animals tested were independent when the interval between locations was >10 days. That proportion was the same with shorter intervals of 1 day or less ($\chi^2 = 0.74$, $P = 0.86$). Theoretically, Schoener's ratio should increase with longer intervals, which enables selecting the minimum period when independence is reached (Swihart and Slade 1985). We pooled all animals with a stable home range to check if our data fit that pattern. Schoener's ratio varies from 0.54 to 0.98 for intervals ranging

Table 1.Trapping success of marten (captures/100 trap-nights) in Rapide 7 East (R7E), Rapide 7 West (R7W), and Kinojévis (KINO) blocks.

Block	Status	Period	Trap-nights	Number of captures	Success
R7E	Uncut	Sept 1990	344	19	5.5
		Sept 1991	298	19	6.4
		Mar 1992	16	1	6.3[a]
R7W	Uncut	Sept 1990	705	9	1.3
		Mar 1991	316	3	0.9[a]
		Sept 1991	1075	13	1.2
		Oct-Nov 1991	1120	23	2.0[a]
KINO	Clearcut	Aug-Dec 1992	2120	29	1.4
		Mar 1993	-[b]	19	-[a]
		Oct-Dec 1993	1537	21	1.4
		Feb 1994	-[b]	3	-[a]
Total			7531	159	

[a] Success not comparable because the period or the trapper (private trapper) was different.
[b] No data.

between <1 day to >24 days, with no trend. These results are not unusual. The validity of the Schoener's ratio has been criticized because animals do not move randomly in their home range (McNay et al. 1994) and important biological information might be lost if it is strictly applied (Andersen and Rongstad 1989, Reynolds and Laundré 1990). We conclude from our results that it is not possible to determine a minimum interval to reach independence of observations for most animals and that a shorter time interval has no effect on independence, enabling us to use all locations. Our second test of independence is based solely on distance between successive locations as related to the time interval (Table 2). Distances are not different between all intervals ($P > 0.25$). This result further supports our decision to use all locations for home-range estimation, irrespective of time interval between locations.

Annual home range of the animals examined in the pre-test reached an asymptote after 25 locations for all 4 kernels and 30 locations for the 2 polygons. Winter home ranges reached an asymptote after 15 locations for 3 kernels (75%, 60%, 50%), 20 locations for the 95% kernel, and 25 locations for the polygons. We selected the 60% kernel to describe the area of intense use of the home range in winter because it amounted to about half the size of the 95% polygon, a proportion we assume appropriate to describe that part of the home range more

Table 2. Distance (m) and time interval between successive locations of martens.

Interval (days)	*n*	Distance $\bar{X}$ [a]	SE
<1	57	1340	136
1	682	1309	41
2	87	1355	117
3	93	1608	132
4-6	26	1291	233
7-14	65	1524	130
15-24	34	1254	173
>24	203	1563	79

[a] No means are statistically different from one another according to Scheffe multiple range test ($P > 0.25$).

intensely used. Annual home ranges with fewer than 25 locations and winter home ranges with fewer than 20 locations were tested for an asymptote of the cumulative area as new locations were obtained. The home ranges of most animals with fewer than 15 locations were discarded because they did not reach an asymptote. In both blocks, 34 annual home ranges and 27 winter home ranges were valid. The mean number of locations was 36 (range = 11-58) and 27 (range = 10-34) for annual and winter home ranges, respectively, and the mean period of radio contact was 280 (range = 90-419) and 112 days (range = 53-121). There was no relationship between the size of home ranges and the number of locations or the number of days (Spearman $r = 0.07$-0.31, $P = 0.06$-0.39), indicating no negative bias for animals with less data.

No female had enough locations in the R7 blocks for analysis; hence, comparisons between blocks are limited to males. Home ranges of males were not different between R7E and R7W, nor between both R7 blocks combined and the KINO block ($P > 0.37$, Table 3). Mean annual home ranges were 9.2 ± 1.0 km^2 ($n = 26$) for the 100% convex polygon and 7.7 ± 0.8 km^2 for the 95% polygon. Mean 95% winter polygons were slightly smaller (7.0 ± 0.9 km^2, $n = 20$) and 60% kernels amounted to 3.0 ± 0.4 km^2. Juveniles and adults in the 3 blocks had similar home ranges ($P > 0.56$). Males and females in KINO also had similar home ranges ($P > 0.75$). One juvenile female had a very large home range (100% minimum convex polygon of 35 km^2), but discarding that animal did not result in female home ranges being significantly smaller than those of males ($P > 0.35$). We pooled both sexes to examine if presence of clearcuts or timing of cutting influenced home-range size in KINO. Martens frequenting cutovers had home

Table 3. Size of the home ranges (km^2) of martens in Rapide 7 East (R7E), Rapide 7 West (R7W), and Kinojévis (KINO) blocks, according to sex, use of clearcuts, timing of cutting activities in or near the home range, and age class.

Block, cutover, and age class	Sex	Annual					Winter				
		n	100% polygon		95% polygon		*n*	95% polygon		60% kernel	
			$\bar{x}$[a]	SE	$\bar{x}$[a]	SE		$\bar{x}$[a]	SE	$\bar{x}$[a]	SE
R7											
R7E	M	7	9.1	1.8	7.6	1.3	4	6.0	0.4	3.1	0.4
R7W	M	5	7.1	2.9	6.4	2.6	3	6.0	3.8	2.5	1.5
R7E+R7W	M	12	8.3	1.6	7.1	1.3	7	6.0	1.5	2.8	0.6
KINO	M	14	9.9	1.4	8.2	1.2	13	7.5	1.2	3.1	0.5
	F	8	11.2	4.1	8.3	2.9	7	9.1	3.3	3.1	1.8
	F[b]	7	7.5	2.0	5.6	1.4	6	6.0	1.5	2.3	0.4
No clearcuts used	M/F	10	7.3A	1.8	5.9B	1.4	8	5.3C	1.5	2.1D	0.4
Clearcuts used	M/F	12	13.0A	2.5	10.1B	1.9	12	9.9C	1.9	3.7D	0.6
No active cutting	M/F	9	7.8	2.0	6.1	1.5	8	6.1	1.6	2.3	0.4
Active cutting	M/F	13	12.2	2.4	9.7	1.8	12	9.4	1.9	3.6	0.6
R7+KINO											
Juveniles	M/F	7	11.4	4.5	8.4	3.2	6	8.8	3.3	3.2	0.9
Adults	M/F	16	8.9	1.4	7.5	1.2	13	6.8	1.8	2.7	0.4

[a] Means followed by the same letter are statistically different according to 1-way ANOVA:
A: $P = 0.047$ B: $P = 0.055$ C: $P = 0.046$ D: $P = 0.040$.

[b] Excluding female 104.

ranges almost twice as large as other martens in the KINO block ($P = 0.040$-0.055). The fact that cutting activities were taking place in the home range or the adjacent area had less influence on the size of home ranges ($P > 0.10$), but the same tendency was apparent with larger home ranges for disturbed martens.

Table 4. Minimum distance (m) per 24 h of marten in Rapide 7 East (R7E), Rapide 7 West (R7W), and Kinojévis (KINO) blocks, according to sex, age class (J: juvenile, A: adult), use of clearcuts, and timing of cutting activities in or near the home range.

Block, cutover, and season	Sex	Age class	*n*	Minimum distance $\bar{x}$[a]	SE
R7					
R7E	M	J/A	67	1250	127
R7W	M	J/A	54	1235	138
R7E+R7W	M	J/A	121	1244 A	93
KINO	M	J/A	347	1467 AB	60
	F	J/A	206	1084 B	69
No clearcuts used	M	J/A	159	1288 C	71
Clearcuts used	M	J/A	188	1617 C	91
No clearcuts used	F	J/A	50	825 D	88
Clearcuts used	F	J/A	156	1167 D	86
No active cutting	M	J/A	97	1253 E	88
Active cutting	M	J/A	250	1549 E	75
No active cutting	F	J/A	91	1168	96
Active cutting	F	J/A	115	1017	98
R7 Fall+winter	M	J	16	1056	204
	M	A	15	884	169
KINO Fall+winter	M	J	82	1361	119
	M	A	77	1531	123
	F	J	45	1247	213
	F	A	30	968	129

[a] Means followed by the same letter are statistically different according to 1-way ANOVA:
A: $P = 0.022$ B: $P < 0.01$ C: $P = 0.055$ D: $P = 0.095$ E: $P = 0.094$.

Minimum distance travelled per 24 h for males was similar between both portions of R7 ($P = 0.62$), averaging 1244 ± 93 m ($n = 121$), a much shorter distance than in KINO (1467 ± 60 m, $n = 347$, $P = 0.022$) (Table 4). In KINO, movements of females (1084 ± 69 m, $n = 206$) were shorter than those of males ($P < 0.01$). During fall and winter, juveniles and adults travelled similar distances in both blocks ($P = 0.26$-0.79). Males ($P = 0.055$) and females ($P = 0.095$) that frequented cutovers increased their daily distance travelled by 25 and 40%, respectively, as compared to other martens in the KINO block. The presence of active cutting operations also tended to increase movements of males ($P = 0.094$) but not of females ($P = 0.18$).

At least 55 (30 males, 25 females) of the 88 collared martens died during our study. This includes 7 cases where only a collar was found but we suspect that the animal could not have removed it, and 5 other cases where the collar was not accessible (underground, in a tree, or under water). If we discard 7 mortalities (2 males, 5 females) related to capture stress that occurred <1 month after collaring, 48 martens died from commercial trapping (16) or natural causes such as injury (6), predation (4), starvation (1), disease (1, probably distemper), and unknown (20). Of the 6 injury cases, 4 were characterized by a broken cranium or large bones and may have been caused by traps set for furbearers; 1 was probably a road kill and 1 was caused by a shotgun. The carcass had been consumed in 6 of the 20 unknown cases, but it was not possible to determine if a predator had killed the animal. Juveniles were more susceptible to natural mortality than adults (0.39 ± 0.15 *versus* 0.28 ± 0.09 per year, $P < 0.01$). Natural mortality rate of females collared in R7 was extremely high compared to that of males (0.99 ± 0.04 *versus* 0.36 ± 0.09 per year, $P < 0.01$), but was similar for both sexes in KINO (0.48 ± 0.15 *versus* 0.46 ± 0.11 per year, $P = 0.36$). Comparisons between blocks are therefore limited to males because data from females in R7 were most likely influenced by the excessive weight of the collar. Collared males living in R7 had a lower natural mortality rate than those in KINO (0.31 ± 0.10 *versus* 0.38 ± 0.12 per year, $P < 0.01$). Trapping mortality rates were 0.20 ± 0.07 per year in R7 and 0.00 in KINO because trapping of marten was suspended by the trapper. A lower proportion of males dispersed from the controls (dispersal rate = 0.16 ± 0.08 per year) than from the treated block (0.32 ± 0.12 per year) ($P < 0.01$). For the 3 blocks combined, survival rate was much lower for dispersing males (0.21 ± 0.17 per year) than for non-dispersing males (0.53 ± 0.17 per year) ($P < 0.01$). Compared to adult males, juvenile males dispersed at a higher rate (0.63 ± 0.18 *versus* 0.10 ± 0.07 per year, $P < 0.01$).

In the control stands, relative density of snowshoe hares steadily declined (22.0 ± 2.9 pellets/plot in 1991, 5.3 ± 0.7 in 1994) (Fig. 3). In the treated stands, numbers of hares were similar to those in the control stands during the 2 years before cuttings ($P = 0.88$). Hares became almost absent from these plots in years 1 (0.2 ± 0.1) and 2 (0.7 ± 0.2) after they were clearcut, a significant decrease compared to controls ($P < 0.01$)).

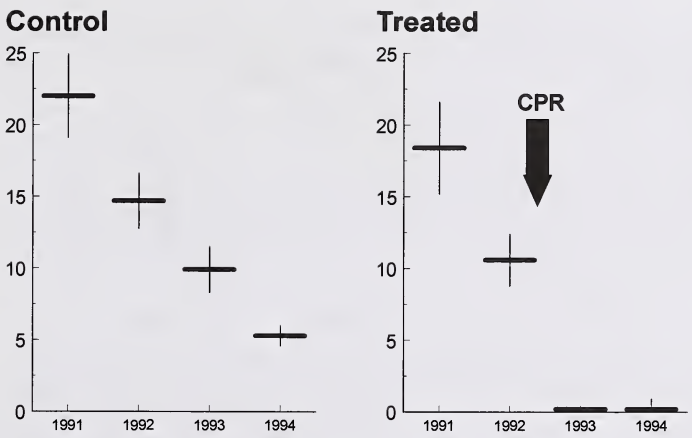

Figure 3. Mean numbers of hare pellets per plot (± SE) from 1991 to 1994 in 5 control and 5 treated stands in the Rapide 7 blocks. The treated stands were clearcut by the CPR technique after the 1992 survey.

Red-backed voles and deer mice represented 47% and 28%, respectively, of the 917 captures of small mammals. Other species encountered were striped and least chipmunks (*Tamias striatus* and *T. minimus*) (106 captures), masked shrew (*Sorex cinereus*) (59), Cooper's lemming (*Synaptomys cooperi*) (23), red squirrel (*Tamiasciurus hudsonicus*) (17), northern flying squirrel (*Glaucomys sabrinus*) (9), short-tailed shrew (*Blarina brevicauda*) (6), least weasel (*Mustela nivalis*) (4), meadow jumping mouse (*Zapus hudsonius*) (3), and meadow vole (*Microtus pennsylvanicus*) (3). Although low numbers preclude statistical analysis for these minor species, we note that northern flying squirrels disappeared from the treated grids after cutting, whereas meadow voles were captured in the treated grids only after logging took place.

Captures of red-backed voles were stable in the control grids from 1990 to 1992 ($\bar{x}$ = 5.5 ± 0.7 captures per grid) and declined 50% thereafter (2.9 ± 0.7) (Fig. 4). Treated grids had relative densities similar to controls in 1990 and 1991 (6.0 ± 0.7) (P = 0.75). The decline in these grids began in 1992, immediately after cutting, and appears more severe than in the controls, but differences are not significant when we compare absolute numbers (P = 0.91). For each grid, we have computed a relative level for each post-treatment year, based on pre-treatment captures:

$$\text{level}_{\text{yeari}} = (2 \times \text{captures}_{\text{yeari}}) / (\text{captures}_{1990} + \text{captures}_{1991}).$$

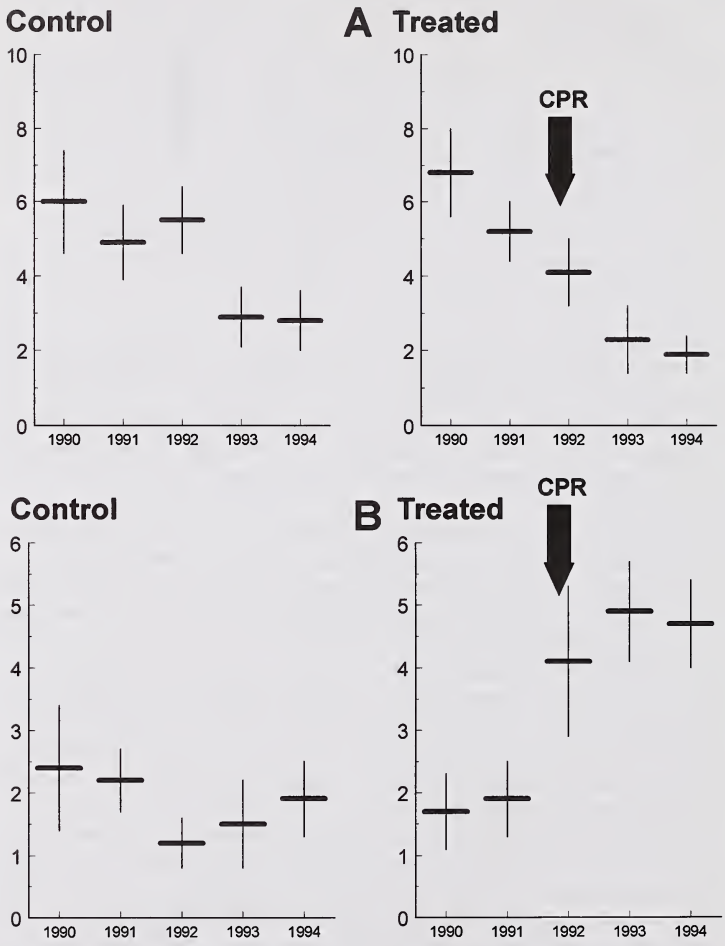

Figure 4. Mean numbers of red-backed vole (A) and deer mouse (B) captures per grid (± SE) from 1990 to 1994 in 5 control and 5 treated stands in the Rapide 7 blocks. The treated stands were clearcut by the CPR technique before the 1992 survey.

Compared to controls, this level is significantly lower in the treated grids in 1992 (0.69 ± 0.14 vs. 1.31 ± 0.23, $P = 0.04$) but not in 1993 ($P = 0.54$) or 1994 ($P = 0.61$).

Captures of deer mice per grid were similar between control (2.3 ± 0.7) and treated stands (1.8 ± 0.4) in 1990 ($P = 0.90$) and 1991 ($P = 0.56$) (Fig. 4). Captures in the control grids from 1992 to 1994 decreased, averaging 1.5 ± 0.4. Conversely, a sharp increase occurred on the treated grids (4.6 ± 0.6). The difference in captures is almost significant in 1992 ($P = 0.07$) and significant for the following 2 years ($P < 0.02$).

Discussion

Three of our 4 hypotheses about the impact of clearcutting on marten were confirmed. Survival was lower in the treated blocks and animals frequenting cutovers had larger home ranges and longer movements. However, trapping success, the index of marten density, was not lower in KINO than in R7E. Our hypothesis that prey abundance would decrease was confirmed for snowshoe hare and, to a lesser degree, red-backed vole, but was denied for deer mouse and total small mammals.

Trapping success for marten in KINO (1.4 captures/100 trap-nights) was about the same as that of commercial trappers in Laurentides Reserve, Quebec (Fortin and Cantin 1990), a large area of moderate density for marten. Katnik et al. (1994) reported a slightly higher success (1.6) in a low density area in Maine, but Soutiere (1979), also in Maine, and Lofroth (1993), in British Columbia, had much higher success (2.7-3.9). A trapping success >5 captures/100 trap-nights, as we encountered in R7E, was obtained in 3 out of 7 studies reported by Lofroth (1993). The biological relevance of difference in trapping success among studies connot be assessed because trapping success is influenced not only by the density of martens but also by many other variables (e.g., equipment, technique, experience of the crew, season). For example, killing traps set in wooden boxes used by commercial trappers are about twice as efficient as live-traps (Naylor and Novak 1994). However, these biases should be consistent within a study. In the 3 blocks that we studied, traps were not distributed systematically and none were set in open cutovers in KINO. Our data in the KINO block indicate that martens were present in the remnant forest patches and forested corridors, but these data have limited utility for estimating density of martens. Although we don't have capture rates before cutting in KINO and trapping success was moderate thereafter, it is probable that marten density decreased following clearcutting because martens were absent from some large clearcuts. Home ranges were larger for martens frequenting cutovers than those for martens living in uncut forest in KINO, and natural mortality and dispersal rates were higher in KINO than in R7.

The decrease in density of martens in KINO after logging is likely less than the 90% decrease reported in Ontario (Thompson 1994) and may be nearer to the 66% decrease estimated in Maine by Soutiere (1979). The density in KINO would have been lower if the commercial trapper in that block had continued trapping.

Annual natural mortality rates of males in R7 and KINO were similar to the 0.35 rate for both sexes computed through life tables by Fortin and Cantin (1990) in Laurentides Reserve. Few such rates are available in the literature. Hodgman et al. (1994) reported 0.12 for males and 0.39 for females from 1 May to 15 December in Maine. Thompson (1994) obtained rates of 0.155 and 0.108×10^{-2}/day [0.43 and 0.33 annual rates] in Ontario. Bissonette et al. (1989) estimated the natural mortality rate of marten was 0.36 for both sexes in Newfoundland. The natural mortality rate of females in R7 was unusually high and is most likely due to the excessive weight of the collar (42 g, 7% of body mass). Although 40-g collars are commonly used for males, collars weighing 22-30 g are more typical for females (Steventon and Major 1982, Davis 1983, Bateman 1986, Brainerd et al. 1994, Hodgman et al. 1994, Sherburne and Bissonette 1994, Thompson 1994). Most studies on the effects of radio-collars on animal activity and survival have involved birds or small mammals, but very few involve larger animals (White and Garrot 1990). A maximum limit of <4% of the body weight of the animal has been suggested by Voigt and Lotimer (1981, in Strickland and Douglas 1987). Collars placed on females in KINO represented <5% of the body weight and apparently were acceptable because mortality rate decreased to a rate similar to males. We recommend a strict adherence to a 4-5% upper limit.

Sanderson (1966) and Buskirk and McDonald (1989) suggested that the size of the home range is inversely related to the habitat quality. This relationship has been documented for birds, notably capercaillie (*Tetrao urogallus*) (Rolstad 1991). Our data in KINO are consistent with this relationship because martens using cutovers have home ranges almost twice as large as those living in areas without cutovers. In Ontario, Thompson and Colgan (1987) reported that size of home range was greater in areas with clearcuts than in areas without clearcuts. The size of home ranges (100% minimum convex polygons) varies among studies, ranging between 1 and 15 km^2, and is usually larger for males (Buskirk and McDonald 1989). Our data for males in R7 and KINO, in areas without cutovers, are among the high values reported and might be related to the lower habitat quality of eastern boreal forests, compared to western forests.

Martens are very mobile animals. Data reported by Bateman (1986) and Taylor and Abrey (1982) indicate that daily movements may often exceed 5-6 km. This distance is much longer than the 1.2-1.5 km average minimum distances per 24 h travelled by males in R7 and KINO. Measurement of a minimum distance assumes linear movement between 2 points. Because martens move in

a zigzag pattern (Snyder and Bissonette 1987), a straight-line computation is biased low (Laundré et al. 1987). Despite the inherent bias, average daily distances travelled by martens in our study area are 25-40% longer in cutovers than in uncut forests. This additional movement would likely incur greater energy expenditures as well as increase the risk of predation to martens inhabiting cutovers.

Snowshoe hares were declining and probably reached the low point of their cycle during our study. Harvest statistics of hares from 1979 to 1994 for the neighboring region of Saguenay-Lac Saint Jean indicate that the high abundance years in the hare cycle were 1980 and 1989, with lows in 1984 and 1994 (Qué. Minist. Environ. et Faune, unpublished data). This cycle strengthens differences due to clearcutting because martens are more vulnerable when prey are scarce (Thompson and Colgan 1987). Although hares disappeared from treated stands in R7, visual observations indicate that hares were still present in some cutovers in KINO. In that block, clearcut black spruce stands appeared to be no more frequented by hare than in R7, but balsam fir and mixed stands that were affected by a spruce budworm outbreak 15-20 years ago had a very dense shrub layer providing abundant cover and browse for hare, even after cutting. Tracking sessions indicated that martens hunted and killed hares (unpubl. data). Microtine rodents are usually the major food of marten, particularly during fall and winter (Strickland and Douglas 1987). Snowshoe hare was an important prey in some studies (Raine 1983, Bateman 1986, Slough et al. 1989), notably in Ontario where it ranked first on a weight basis (Thompson 1986; Thompson and Colgan 1990, 1994). This region shares conditions more similar to our study area than areas where microtines are the principal prey of marten.

Presence of marten in cutovers appears strongly associated with residual cover and the presence of snowshoe hare. Although clearcuts with a sparse shrub layer are avoided by martens, preliminary analysis of habitat selection indicates that cutovers with abundant regeneration are frequented (unpubl. data). As marten habitat, these cutovers might be functionally more similar to partial cuts than they are to clearcuts. Marten can be maintained in partial cuts (Major 1979) and in areas where groups of trees and woody debris are left after cutting, such as recommended by Hargis and McCullough (1984) to preserve marten habitat. Such habitat contains sufficient cover against predators and still supports snowshoe hares.

Because clearcutting typically does not provide habitat conditions suitable for hare immediately after cutting (Ferron et al. 1994), we conclude that large clearcuts in the boreal forest, even with the CPR technique, have negative effects on marten densities and survivorship. According to Thompson and Harestad's (1994) model, marten density should decrease rapidly when more than 20-30% of the landscape is cut by dispersed removal. Our results indicate that some

animals had home ranges that included up to 50% clearcut areas. We suggest that martens are more tolerant to forest fragmentation than was previously accepted. More detailed analyses of our data with respect to time and spatial scales are needed to define landscape mosaics, in terms of residual forest, that would leave suitable habitat for marten after clearcutting.

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